# *ARCHAEORADIOLITES*, A NEW GENUS FROM THE UPPER APTIAN OF THE MEDITERRANEAN REGION AND THE ORIGIN OF THE RUDIST FAMILY RADIOLITIDAE

*by* MUKERREM FENERCI-MASSE*, JEAN-PIERRE MASSE*, CONSUELO ARIAS† *and* LORENZO VILAS†

*Centre de sédimentologie-paléontologie, laboratoire associé au CNRS, Université de Provence, 13331 Marseille Cedex 03, France; e-mails: mmasse@up.univ-mrs.fr; jpmasse@up.univ-mrs.fr

†Departamento de Estratigrafia, Instituto de Geologia Economica (CSIC-UCM), Facultad de C.C. Geologicas, Universidad Complutense, 28040 Madrid, Spain; e-mails: ariasc@geo.ucm.es; vilasl@geo.ucm.es

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**Abstract:** *Archaeoradiolites* gen. nov. (Radiolitidae), mainly characterized by radially arranged branching walls structuring the outer shell layer, includes two species, *Archaeoradiolites primitivus* gen. et sp. nov. and *Archaeoradiolites hispanicus* gen. et sp. nov. (type species), the distinction of which is based on size, shell habit and development of the radially branching microstructure. Their geographical distribution is restricted to south-east Spain and south-west France, i.e. the Western European Tethyan margin, whereas data from the Black Sea coast of Turkey suggest a possible extension to the Eastern European Tethyan margin. Each species has a distinct biostratigraphic distribution within the Upper Aptian (mainly the Gargasian). *Agriopleura* is suggested to be the direct ancestor of *Archaeoradiolites*, which in turn is considered as the progenitor of *Eoradiolites*. The onset of the Radiolitidae is associated with global oceanic changes that favoured calcite as opposed to aragonite biomineralization. The acquisition of a porous shell microstructure appears, in many respects, biologically advantageous and may account for gaining a rapid (< 1 myr) ecological ability for efficient colonization and occupation of space of the family in the earlier phase of its radiation.

**Key words:** rudist bivalves, Upper Aptian, new genus, biostratigraphy, evolution.

THE Late Aptian–Albian marked the onset of the radiation of Radiolitidae, which followed the mid-Aptian crisis that affected shallow water, carbonate platform biotas, including rudists (Masse 1989; Masse and Gallo-Maresca 1997). This family is characterized by specific attributes regarding: (1) shell structure: the calcitic outer shell layer tends to exhibit a cellular microstructure, with various geometrical patterns; (2) myocardinal features: myophores of the left valve (LV) are represented by vertical, downward-projecting plates into the right valve (RV), teeth are nearly equal and also project deeply in sockets or gutters of the opposite valve.

The so-called cellular structure has been attributed by earlier workers (Palmer 1928; Böggild 1930; Douvillé 1935; Milovanovic 1935; Masse and Philip 1972; Strum and Perkins 1975; Amico 1977) to the association of two distinct sets of laminae or plates: the funnel plates, here labelled plates, conforming with the overall conical outer shell habit, and the radial plates, muri or walls, that are orthogonal to the plates, here labelled walls. Walls represent salient infoldings of the plates. This organizational mode is found, for instance, in *Eoradiolites davidsoni* (Hill) and other, relatively advanced, forms of the genus *Eoradiolites*, and also in some species of *Praeradiolites* and *Bournonia*, forms in which the resulting, cellular pattern is mainly quadrangular (Amico 1977). The polygonal cell geometry of the Sauvagesiinae relates to the same process (Milovanovic 1935) whereas this group has been considered as a division of the Radiolitidae (Douvillé 1902).

Cellular structures belonging to the foregoing categories are not observed in all Radiolitidae. For instance, a radial irregular pattern tends to characterize the genus *Katzeria* Sliskovic (Sliskovic 1966; Caffau *et al.* 1992; Pejovic 2002), while in *Rajka* Milovanovic walls are represented by minute columns (Grubic 2002). Moreover, some Radiolitidae lack any type of cellular porous

microstructures, as in *Gorjanovicia* Polsak (Polsak 1967), which has a compact outer shell, similar to that of the Monopleuridae.

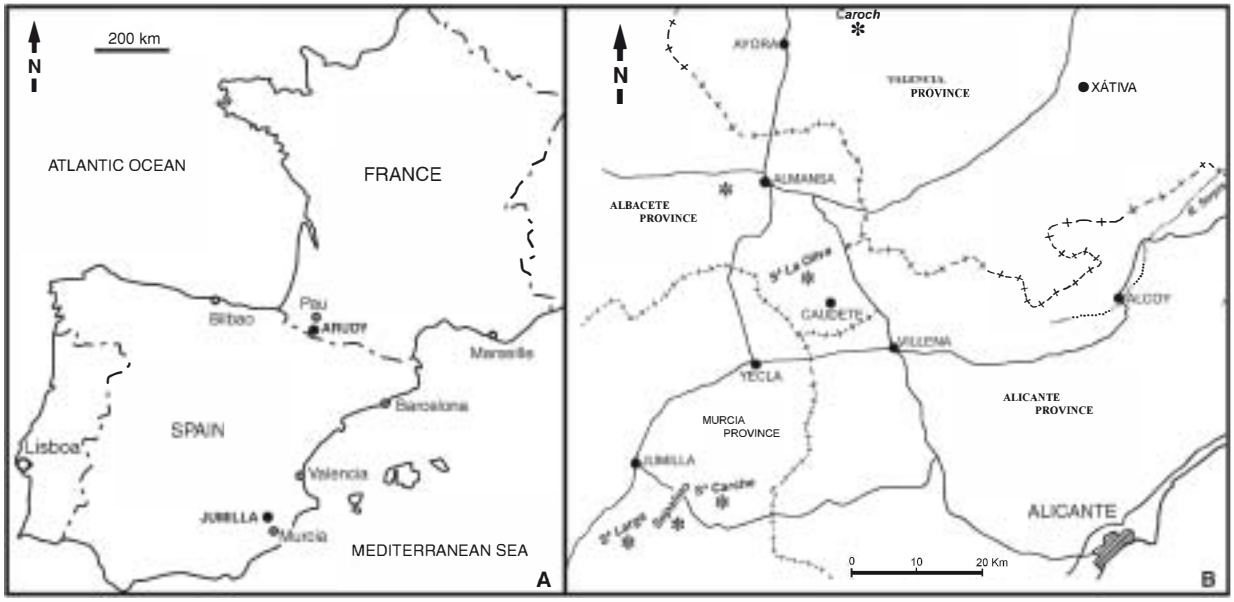
The objective of the present paper is to describe a new genus, *Archaeoradiolites*, found in the Upper Aptian of south-east Spain, characterized by a radially branching outer shell microstructure, which departs from that observed in other Radiolitidae, especially the subcontemporaneous *Eoradiolites*. The form here described has been formerly ascribed to *Eoradiolites*, essentially *Eoradiolites plicatus* (Hill) (Gallo-Maresca 1993; Masse 1995; Masse *et al.* 1998). Identical or closely related forms have also been reported from south-west France (Masse 1995) (Text-fig. 1A) and the western Black Sea region of Turkey (Masse *et al.* 2002). Because the new taxon is the oldest Radiolitidae documented until now and has potential to be the root of the family, we discuss its relationships with both the progenitor of the Radiolitidae, the genus *Agriopleura* Kühn, and the genus *Eoradiolites* Douvillé, formerly regarded as the origin of the family.

## STRATIGRAPHY OF THE RUDIST-BEARING BEDS FROM SOUTH-EAST SPAIN

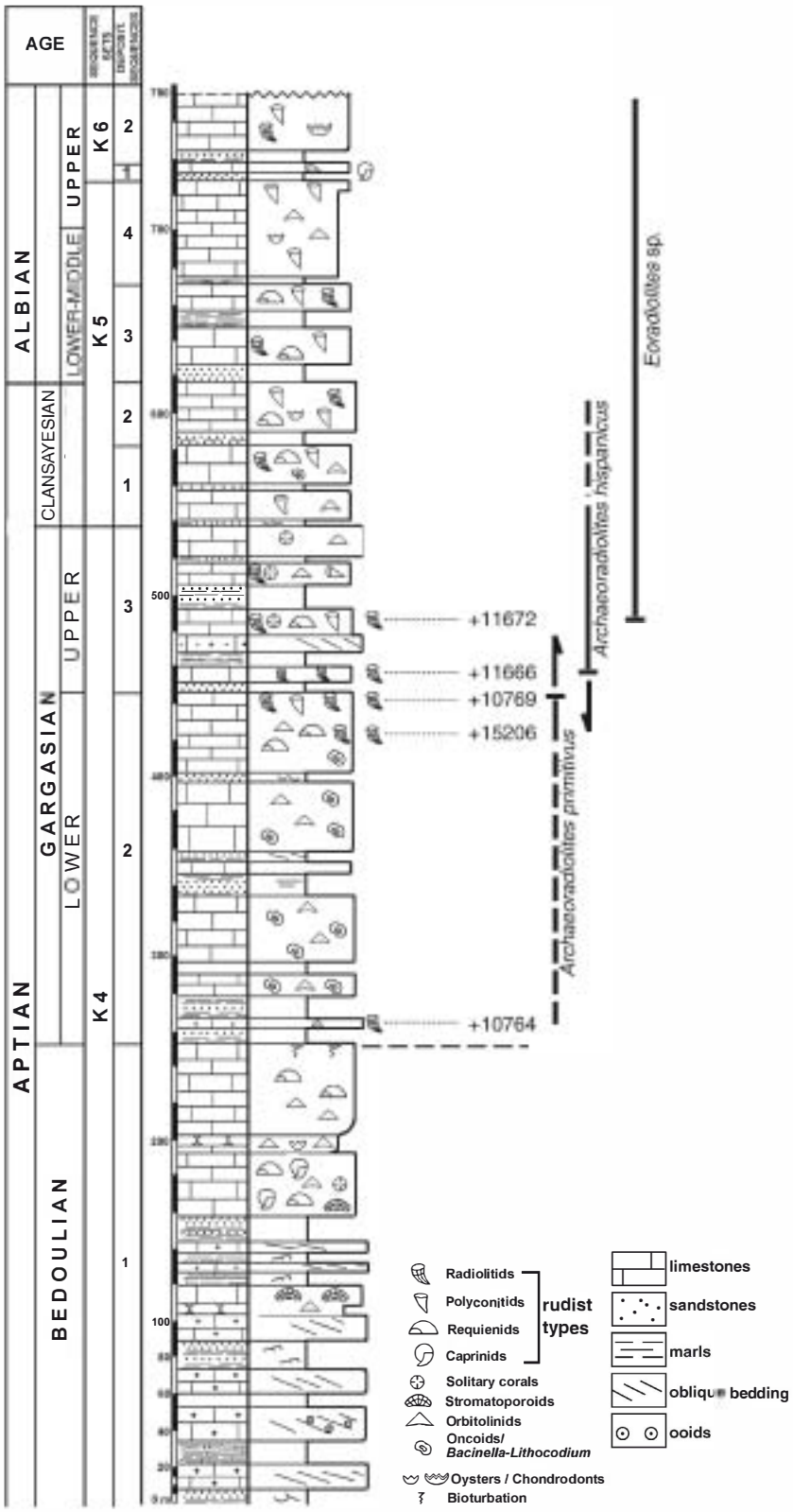
Radiolitidae have a significant record in the Late Aptian–Albian of south-east Spain where they have been reported from various localities distributed in the Alicante, Valencia, Albacete and Murcia provinces (Arias *et al.* 1989, 1993, 1996; Masse *et al.* 1992, 1998; Gallo-Maresca 1993, in press) (Text-fig. 1B). The following will focus on Late Aptian radiolitid-bearing beds where specimens of *Archaeoradiolites* have been collected, mainly the Almansa-Jumilla region, including the Carche (Masse *et al.* 1992), Sopalmo (Arias *et al.* 1996), Sierra Larga, La Oliva, Caroch series, where the stratigraphic distribution of rudists has been calibrated to benthic foraminifera, essentially Orbitolinidae, having potential for distinguishing the lower and upper part of the Gargasian, and the Clansayesian.

The synthetic stratigraphic section of the Sierra del Carche (Aptian–Albian) (Text-fig. 2) illustrates the stratigraphic distribution of the two species of *Archaeoradiolites* and also *Eoradiolites*, in the Gargasian–Clansayesian interval. The biostratigraphic interpretation that conforms to the Masse *et al.* (1992) former dating can be summarized as follows: (1) *Orbitolina* (*Mesorbitolina*) *pervia* Douglass and *Dictyoconus*? *pachymarginalis* Schroeder mark the Lower Gargasian; (2) *Orbitolinopsis*? *aquitanica* Schroeder and Poignant and *Orbitolinopsis reticulata* Moullade and Peybernes identify the Upper Gargasian; (3) *Pseudochoffatella cuvillieri* Deloffre marks the Clansayesian.

The tripartite division of the Upper Aptian, based on specific micropalaeontological assemblages, is well documented on a regional scale (Arias *et al.* 1993, 1996) and is corroborated by sequence analysis. The Lower/Upper Gargasian boundary is marked by a major sedimentary discontinuity: a subaerial truncation surface followed by marginal marine or continental sands and sandstones (the so-called Montemayor sands), with a wide regional extent.




**TEXT-FIG. 1.** A, radiolitid-bearing locations in south-west France and south-east Spain. B, radiolitid sites in the Valencia-Albacete and Murcia provinces in south-east Spain (stars indicate fossil-bearing localities).




**TEXT-FIG. 2.** Stratigraphic section of the Aptian–Albian of the Sierra del Carche showing the position of *Archaeoradiolites* species and the FO (first occurrence) of *Eoradiolites*.

Aside from *Archaeoradiolites* these stratigraphic sections also document the FO (first occurrence) of *Eoradiolites* sp. *sensu stricto*. Associated rudists consist of *Pseudotoucasia santanderensis* (Douvillé), *Horiopleura* gr. *almerae* Paquier and *Polyconites verneuili* (Bayle).

## SYSTEMATIC PALAEONTOLOGY

The symbols used in the descriptions are as follows: LV, left valve; RV, right valve; D, dorsal side; V, ventral side; A, anterior side; P, posterior side; AVc, anteroventral carina; amp, anterior myophoral plate; pmp, posterior myophoral plate; mp, myophoral plate; at, anterior tooth; pt, posterior tooth; as, anterior socket; ct, central tooth; ps, posterior socket; L, ligament ridge; Ab, anterior band; Pb, posterior band; Ib, interband.

Size estimates include dDV, the dorsal-ventral diameter, and dAP, the antero-posterior diameter of the RV, the average diameter being (dDV + dAP)/2.

Order HIPPURITOIDA Newell, 1965
Superfamily HIPPURITOIDEA Gray, 1848
Family RADIOLITIDAE d'Orbigny, 1847

Genus ARCHAEORADIOLITES gen. nov.

*Type species.* *Archaeoradiolites hispanicus* gen. et sp. nov.

*Derivation of name.* Greek *archaeo*, ancient, and radiolitid, intended to imply that the genus is considered a primitive member of this group.

*Diagnosis.* Conical RV and flat LV. Outer shell microstructure consisting of radially arranged branching walls. Plates virtual, formed by adjoining inflated terminations of the radial walls. Anterior band flattened, moderately salient, interband depressed, posterior band rounded and salient. Ligament ridge present, myophoral organization conforming to the radiolitid type. LV with a laminated concentric structure.

*Discussion.* The definition of *Archaeoradiolites* gen. nov. focuses on two main attributes of the RV: radially arranged branching walls, and virtual plates. None of the Radiolitidae described until now possesses these two characters. *Eoradiolites* has a typical cellular quadrangular structure, which consists of the combination of walls and plates (Douvillé 1902, 1909; Amico 1977; Coogan 1977; Gallo-Maresca 1993) (Text-fig. 3). *Praeradiolites* and *Sphaerulites* also display a cellular structure (Douvillé 1902; Milovanovic 1935; Dechaseaux *et al.* 1969; Amico 1977). *Katzeria* is the only form having a radially arranged outer shell architecture (Sliskovic 1966; Caffau *et al.* 1992; Pejovic 2002), whereas in this genus the radial walls are very thick, branching appears irregular (pl. 2, fig. 1 in Caffau *et al.* 1992) and mainly restricted to the inner shell margin (pl. 4, figs 1, 3 in Pejovic 2002). Moreover *Katzeria* lacks a ligamental ridge and possesses pseudopillars (Sliskovic 1966). Radial structures are locally present (i.e. dorsal side) in *Petkovicia*? *verajana* Sliskovic, figured by Steuber (1999) whereas the overall organization is cellular, i.e. built after walls and plates.

*Archaeoradiolites hispanicus* gen. et sp. nov.
Text-figures 3A, 4–16

1992 *Eoradiolites* sp.; Masse *et al.*, pp. 209–201, pl. 4, fig. 7.
1993 *Eoradiolites katzeri* Sliskovic; Gallo-Maresca, p. 34, pl. 2, figs 2, 4.
1993 *Eoradiolites plicatus* (Conrad); Gallo-Maresca, pp. 55–56, pl. 7, fig. 1.
1998 *Eoradiolites plicatus* (Conrad); Masse *et al.*, p. 206, fig. 13-1.

*Derivation of name.* From Hispania, the ancient Roman name of Spain.

*Type locality.* Sopalmo, south-east of the city of Jumilla, Province of Murcia (south-east Spain) (Text-fig. 1B); lat. 38°24′58″N, long. 1°14′48″E.

*Holotype.* In the two slabs from sample 12077 from Sopalmo (Text-figs 4–5), which contains 15 serial transverse sections of conjoined RVs; the holotype is labelled 12077-1; the slab and associated thin section are housed with other materials in the Centre de Sédimentologie-Paléontologie, Université de Provence, Marseille.

*Paratypes.* Sample 12077, adjacent individuals (labelled 12077-2–15) from the above-mentioned slab; samples 11666 from the Sierra del Carche, 12091 from Sierra Larga (an isolated specimen) and 12079 (eight isolated juvenile specimens) from Sopalmo.

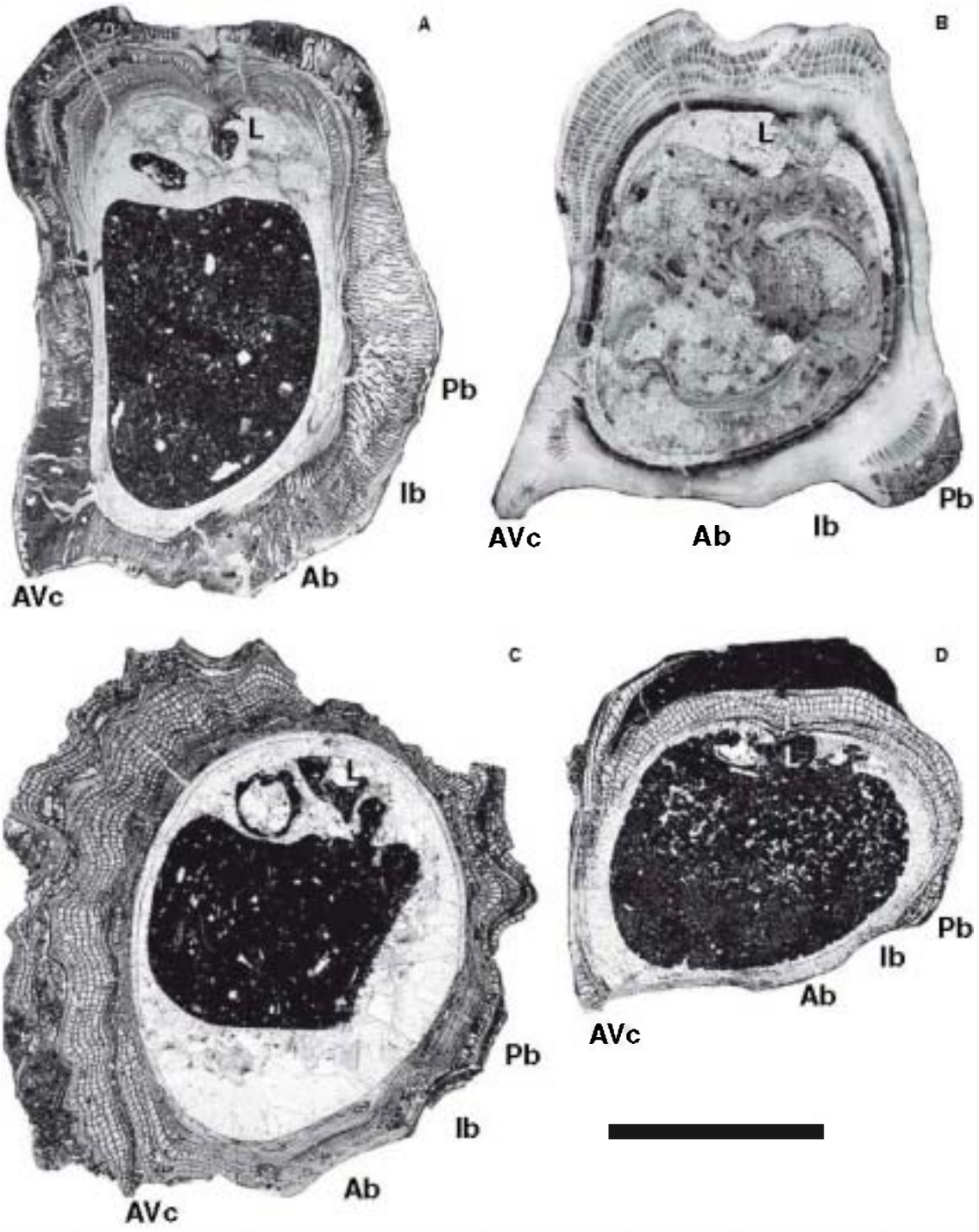
*Additional material.* Sample 10920, a slab including 11 serial transverse sections from Almansa.

*Diagnosis.* Moderate size [max dDV = 31 mm, dAP = 25 mm; average diameter (dDV + dAP)/2 = 15 mm], conical, strongly foliated *Archaeoradiolites*. Radial branching structure mainly developed on dorsal side, usually extending to anterior and posterior sides and less frequently on ventral side. Shell foliae recording stepwise ontogenetic variations regarding development of radial structure. Accordingly during growth, radial bands change from compact to septate, the anterior flat and wide, the posterior salient and located at the posteroventral edge, the interband depressed. LV with concentric porous, laminated structure. Ligament ridge short with a trapezoidal outline and concave termination.

### *Description*

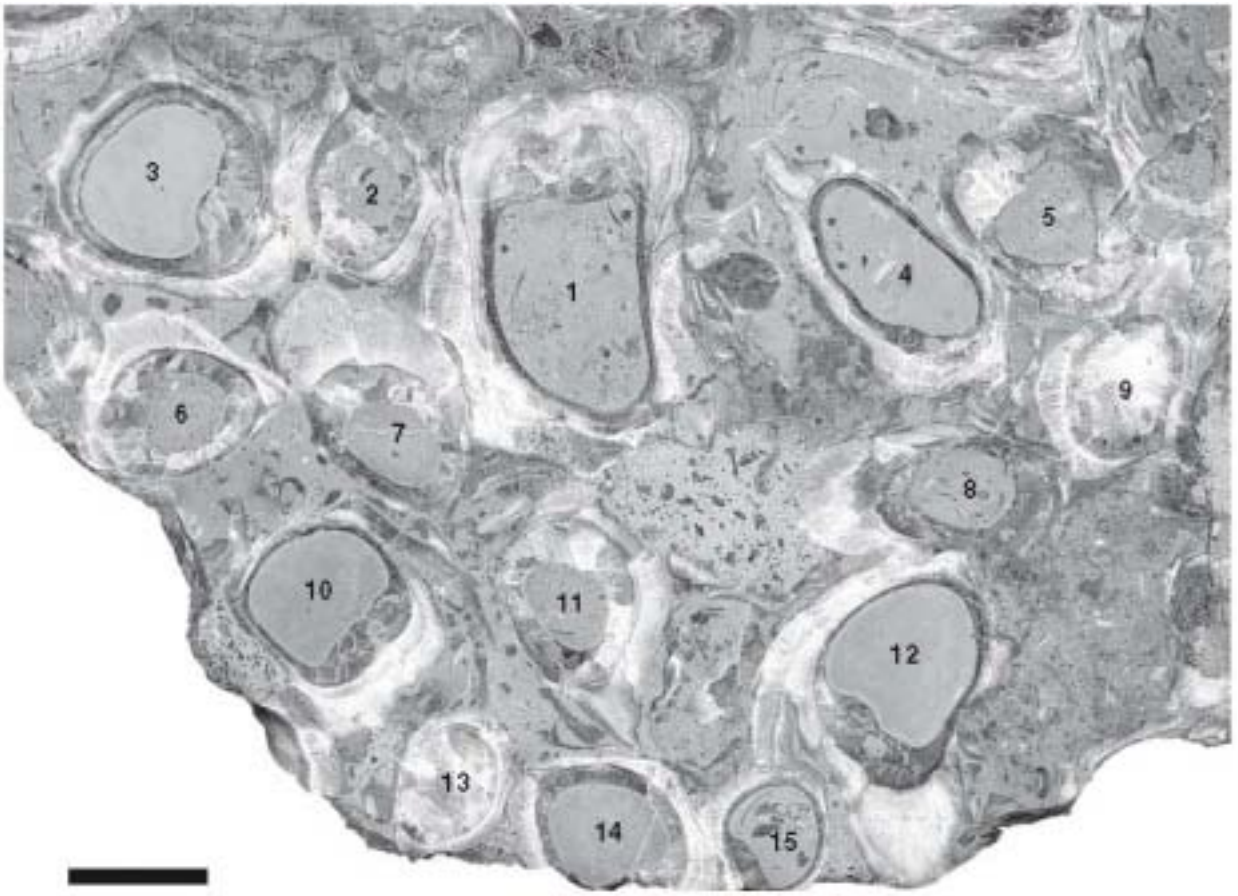
*External characters.* Data from transverse and longitudinal sections combined with the observation of isolated specimens lead to the following description.

RV conical, arcuate and slightly twisted at juvenile stage becoming straight in adult stage, except in dense aggregations




**TEXT-FIG. 3.** Tranverse sections of typical species of Upper Aptian–Albain *Eoradiolites* compared with *Archaeoradiolites* gen. nov. A, *Archaeoradiolites hispanicus* gen. et sp. nov., holotype, Sopalmo. B, *Eoradiolites plicatus* (Conrad), Upper Aptian, Lebanon. C, *Eoradiolites* cf. *davidsoni* (Hill), Albian, Bell County, Texas. D, *Eoardiolites katzeri* Sliskovic, Upper Aptian, Staric, Bosnia. A, C and D, collection J.-P. Masse, Marseille; B, Douvillé's material (fig. 74 in Douvillé 1910), Centre commun des collections de géologie (Université Claude Bernard Lyon 1). Scale bar represents 1 cm.

where the orientation of the shell axis may be modified during growth in connection with the available space left by the coeval growth of neighbouring individuals. Transverse shell outline varies from subcircular (juvenile stage) to rhomboidal or quadrangular (adult stage) (Text-fig. 5). The ventral side is usually flattened and the dorsal side rounded or lobate with a longitud-



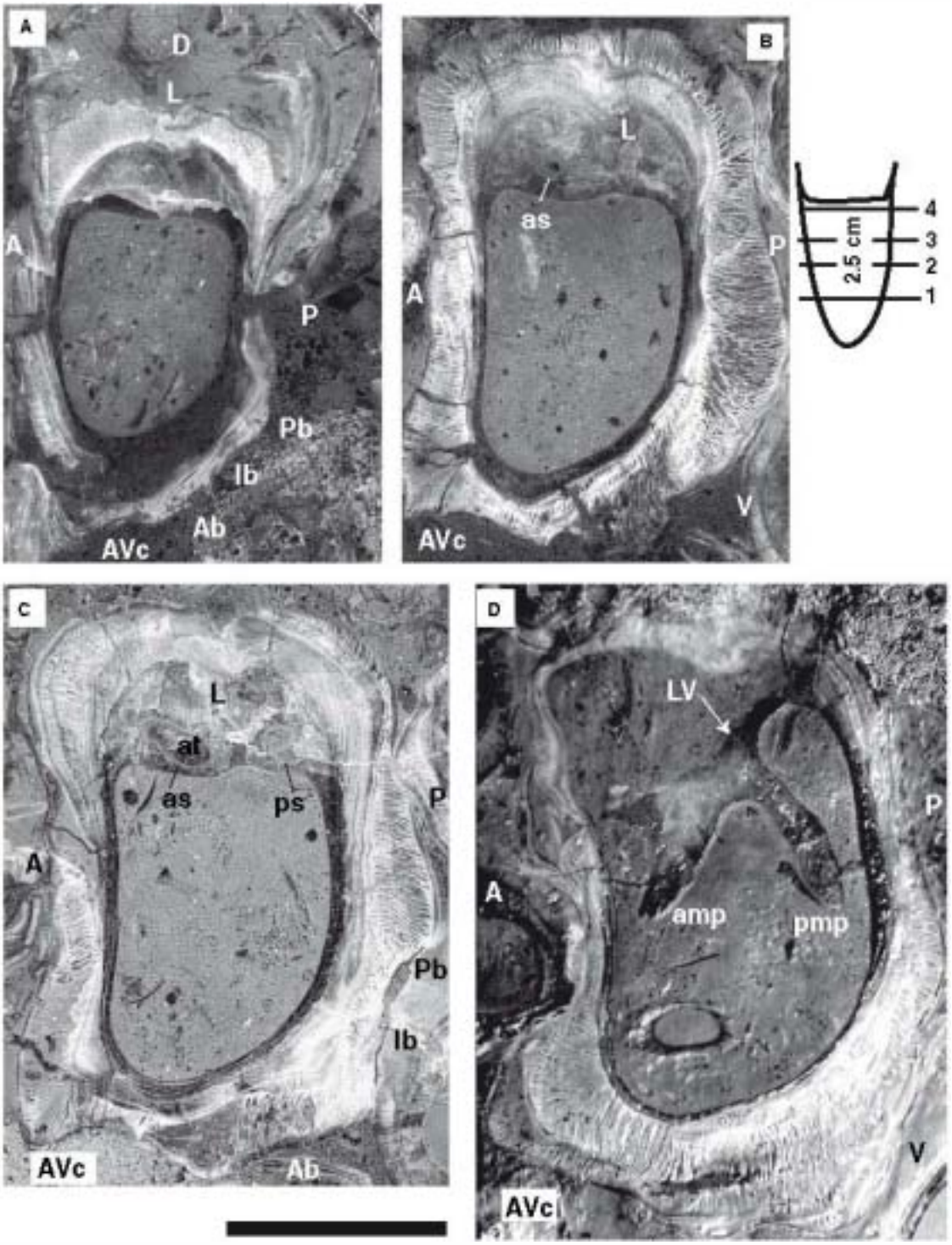

**TEXT-FIG. 4.** Transverse section through a congregation of *in situ Archaeoradiolites* (slab cut parallel to bedding) showing the variability in shell outline, due to shell packing, cardinal features and the outer shell radial microstructure (RV); individuals are labelled from 1 to 15, 1 being the holotype; Sopalmo, sample 12077; scale bar represents 1 cm.

inal median depression where the ligamental groove is located. The transverse development of the anteroventral carina (arête V *sensu* Douvillé 1910) correlates to the overall dorsoventral shell compression (i.e. the elongation of the axis joining the carina to the posterior side) (Text-figs 4, 5, 6B). Shell compression of this kind is found in dense aggregations where shell morphology is modified according to the available space. The conical RV is made of tiered, fitted funnels resulting in foliated morphology (Text-fig. 6A), usually consisting of 4–6 foliae separated by constrictions, the diameter of which increases during successive growth steps; however, the last step in some specimens records some size reduction (Text-fig. 7). Tiering or foliation is mainly developed on the dorsal side (Text-figs 4, 5A, 6A) and tends to invade the anterior then posterior sides during growth, the ventral side being usually smooth except for large specimens at adult stage (e.g. holotype). The growth surface extending from the shell edge to the inner margin of the outer shell (i.e. where the junction with the former aragonitic inner shell layer was situated) slopes inward. Commissural transverse dimensions range from 12 to 25 mm (anteroposterior) and 13 to 31 mm (dorsoventral) (holotype 16–29 mm), whereas the shell height varies from 19 to 35 mm.

The anterior band is represented by a moderately salient, flat (slightly depressed in the middle), wide area (4–6 mm) followed by a depressed interband flanking a salient rounded posterior band located at the junction between the ventral and posterior sides (Text-figs 5, 8). The inner shell margin facing the bands is flattened. Radial bands are well defined in specimens with a compact ventral outer shell layer (Text-fig. 5A) or where radial walls are restricted to the bands (Text-fig. 8). Where the ventral side is totally invaded by the radial walls, bands are fused and consequently more difficult to define (Text-figs 3A, 5D).

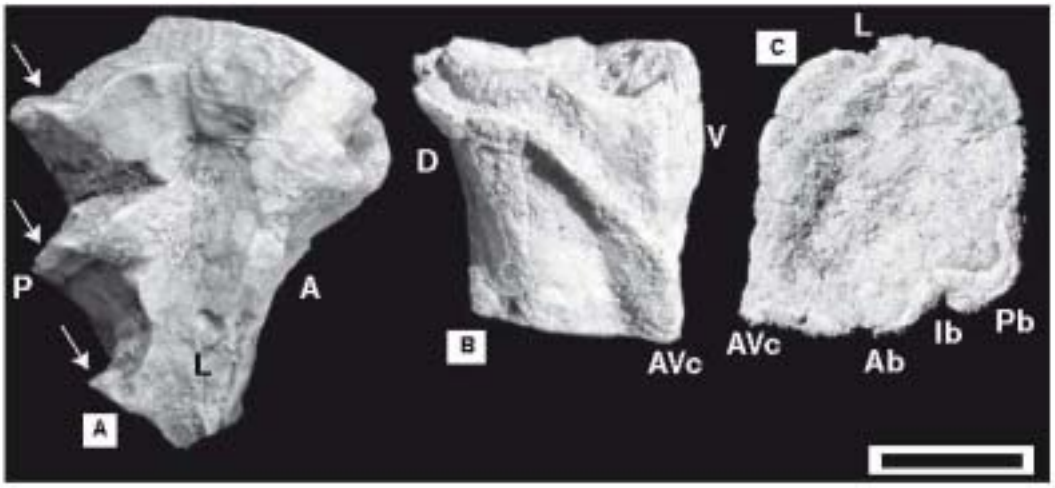
LV flat, slightly depressed dorsally (Text-fig. 9A–B), the margin of which only partially covers the sloping-inward outer shell margin at the opposite valve (Text-fig. 9C). Transverse (Text-fig. 9D) and longitudinal axial sections (Text-fig. 9E) show the laminated concentric structure, frequently obscured by microborings (Text-fig. 9D) or micritization (Text-fig. 9C).

*Internal characters.* The cardinal apparatus of the right valve is convex inward and includes two sockets, the anterior larger than the posterior (Text-figs 3A, 4), the central tooth is lamellar and oblique to the dorsal shell margin (Text-fig. 10). Teeth of the left valve possess an elliptical transverse outline.

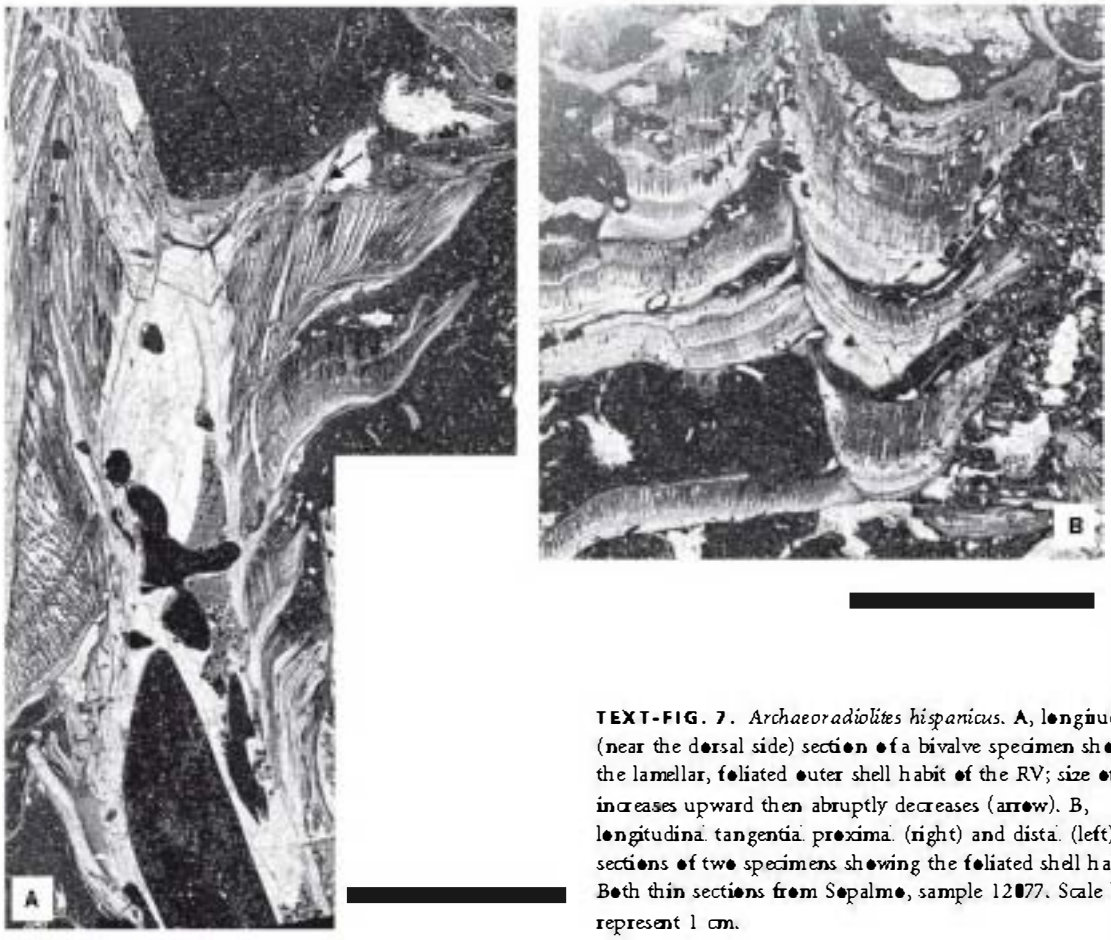



**TEXT-FIG. 5.** *Archaeoradiolites hispanicus*, holotype. Serial transverse sections of the RV showing the overall organization. Note that in A the ventral side has a compact outer shell structure whereas other sections cut in the adult shell portion show radially arranged walls; D displays the myophoral apparatus of the LV projecting into the RV. Scale bar represents 1 cm.

Myophoral plates protrude from the left valve down into the opposite valve with a bull-horn transverse outline; the posterior one is shorter and thicker than the anterior (Text-fig. 11). Ligament ridge with a triangular or trapezoidal transverse outline and a concave end (Text-figs 3A, 10B–C) flanked by a ligamental cavity (Text-fig. 10B–C).

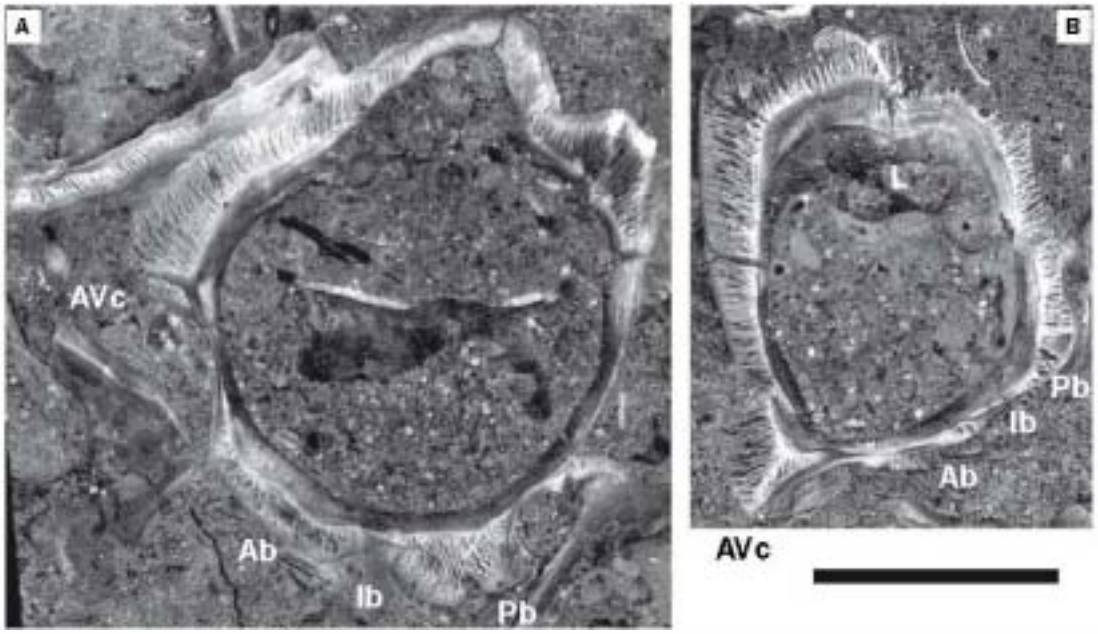



**TEXT-FIG. 6.** *Archaeoradiolites hispanicus*, isolated specimens (RV). **A**, posterior view showing the foliated habit; sample 12091, Sierra Larga, Gargasian. B–C, Sopalmo, sample 12079. B, anterior view. C, apical view showing the transverse outline. See text for explanation of abbreviations; scale bar represents 1 cm.




**TEXT-FIG. 7.** *Archaeoradiolites hispanicus*. **A**, longitudinal (near the dorsal side) section of a bivalve specimen showing the lamellar, foliated outer shell habit of the RV; size of foliae increases upward then abruptly decreases (arrow). B, longitudinal tangential proximal (right) and distal (left) sections of two specimens showing the foliated shell habit. Both thin sections from Sopalmo, sample 12077. Scale bars represent 1 cm.

*Microstructure of the outer shell layer*. The outer shell layer includes compact, banded, locally wavy parts (Text-figs 7, 12–13) and radially arranged walls the geometry of which is revealed by transverse and longitudinal (subaxial and tangential) sections (Text-fig. 13). In transverse section walls radiate from the cortical layer towards the body cavity; convex microbanding

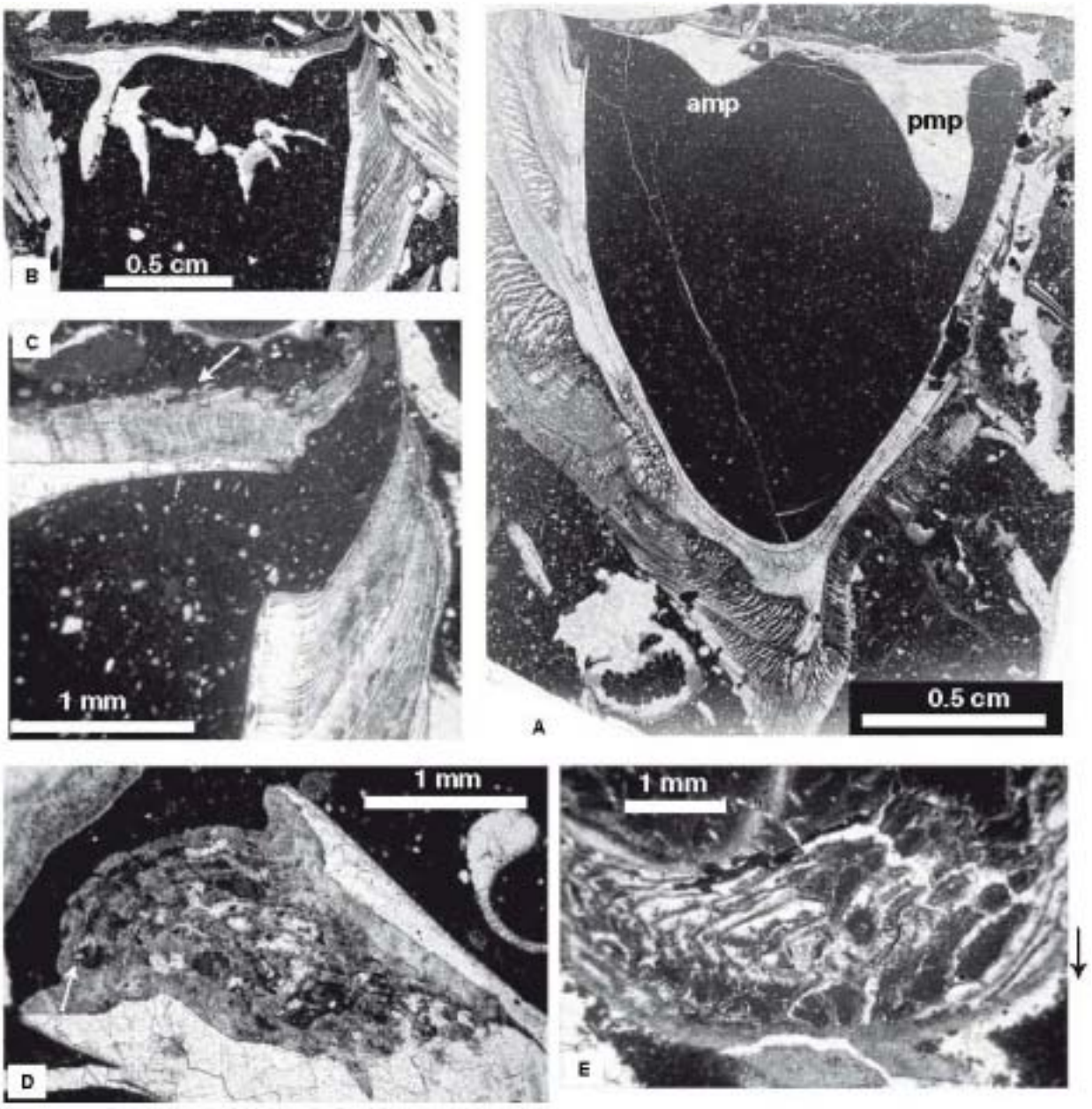



**TEXT-FIG. 8.** *Archaeoradiolites hispanicus*. A–B, transverse sections showing the organization of the radial bands; wide flattened anterior band (Ab) and salient rounded posterior band (Pb) separated by a depressed interband (Ib). AVc: anteroventral carina. Carche, sample 11666. Scale bar represents 1 cm.

conforms to this orientation (Text-fig. 13A–B). Asymmetry and low angle (25–35°) pectinate dichotomy are the characteristic attributes of radiating walls (Text-fig. 13C). In addition to branching, walls exhibit thickness variations during growth as well as coalescence (Text-fig. 13A–C). Bifurcations and microbanding revealed by transverse section look like perostromatic (microbial) organizations of, for instance, the *Epiphyton-Frutexites* group, common in the Palaeozoic (Riding 1987); microbial-like structures have also been documented in constructional cavities of modern oysters (Chinzei and Seilacher 1993). The branching structure is made by vertical radial bifurcated plates, the overall geometry of which departs from bush-like perostromatic accretions, giving limited evidence for microbes to be involved in the formation of the corresponding architecture.

In longitudinal sections running through the body cavity, walls appear discontinuous, a result of the transverse branching pattern (Text-fig. 13D). Each growth band includes a basal cortical layer followed by branching walls limited by a virtual plate (Text-fig. 13A–C). By contrast with plates found in other Radiolitidae (e.g. *Eoradiolites*), especially *E.* gr. *davidsoni*, which consist of laminated or thin fibrous material (Milovanovic 1935; Amico 1977; Gallo-Maresca 1993) (Text-fig. 3C), virtual plates result from adjoined terminations of the radial walls (Text-fig. 13C) delineating subconcentric lines to the inner shell margin (Text-figs 3A, 10A). In transverse sections close to the commissure two or three virtual plates are usually observed. Transverse sections may also include several intersections of cortical layers, with a compact, relatively thick microstructure (Text-fig. 3A). This is due to the rhythmic growth of the shell architecture, including several fitted foliae, each bounded by a basal cortical layer and terminated by a virtual plate. Tangential longitudinal sections show (Text-fig. 13F) parallel walls with variable spacing, a result of the radial branching pattern. At the top of individual foliae, the radial organization is usually open, i.e. not sealed by any cortical-type layer (Text-fig. 13E).

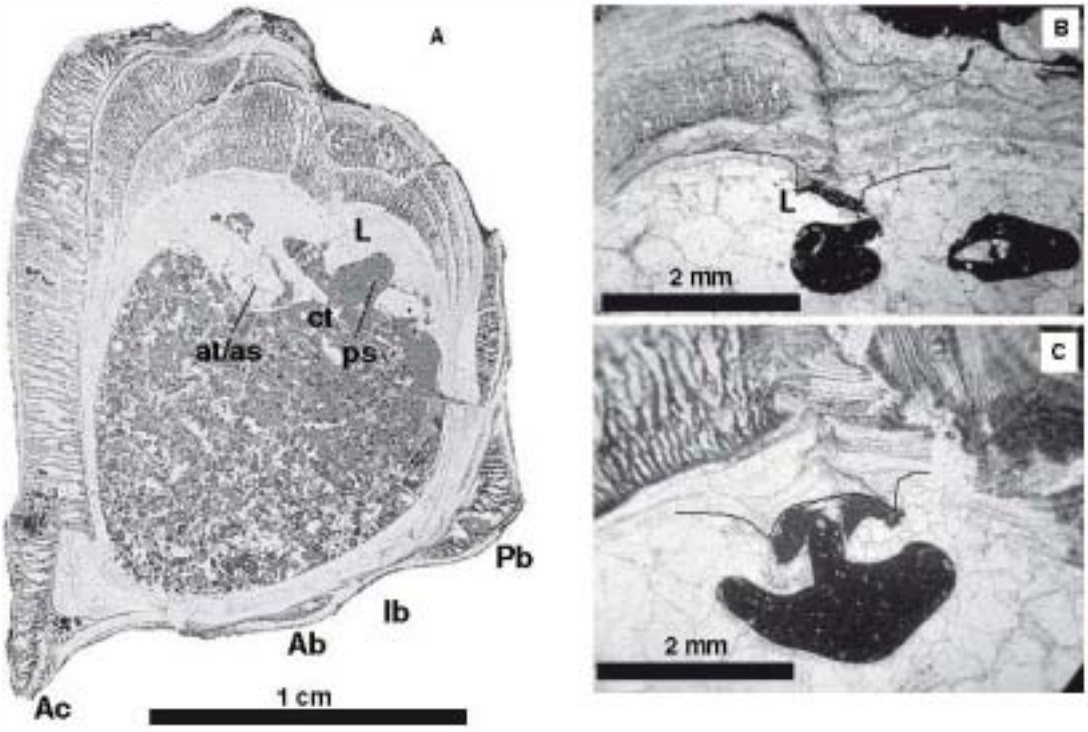
*Discussion.* The shells might have been covered by a conchiolin sheet (periostracum), known to offer some defence against predation by boring (Harper 1994). In a given growth band, quantitative estimates of microrhythms formed by the alternation of micritic and fibrous laminae (doublet fondamental *sensu* Masse and Philip 1972) (Text-fig. 13E, D) document between 20 and 30 alternations. The assumption that a given doublet represents 15 days of growth (Amico 1977; Regidor-Higuera *et al.* 2002) suggests that one folia may have been produced during one year; therefore, an individual with 4–6 foliae may have been 4–6 years old. This life duration does not depart significantly from those reported for Upper Cretaceous Radiolitidae, notwithstanding their larger size (Amico 1977; Steuber 1996). Peeling off the cortical layer for producing lamellar bioclasts appears a typical property of the Radiolitidae (Philip *et al.* 1977; Sanders 1999). *Archaeoradiolites hispanicus* gen. et sp. nov. documents an unusual mode of shell alteration; the radial walls tended to disintegrate into silt-size particles that transferred to the surrounding sediment (Text-fig. 14). The process of disintegration, which needs further investi-



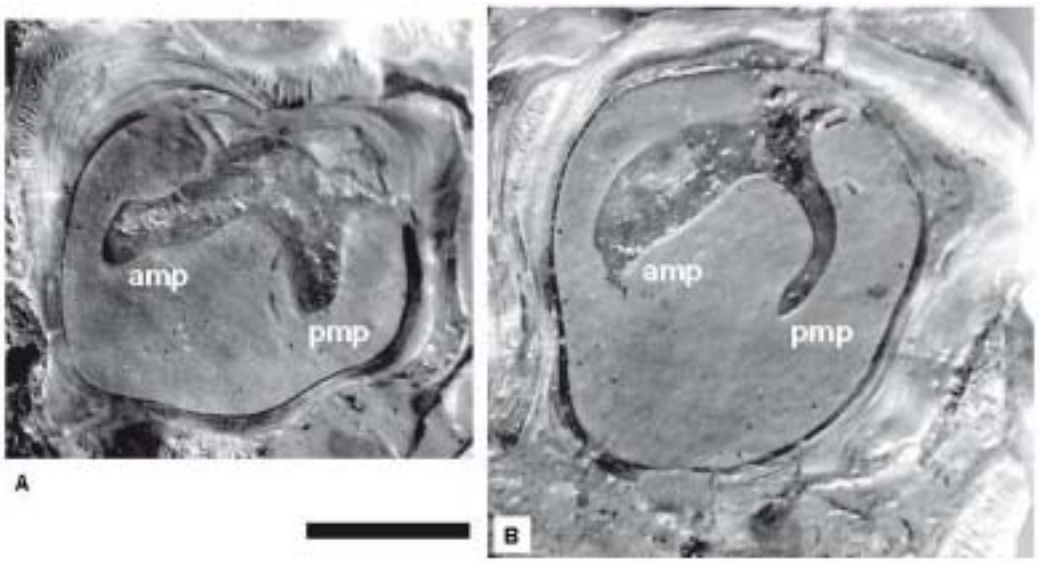

**TEXT-FIG. 9.** *Archaeoradiolites hispanicus*. A–B, longitudinal (nearly anteroposterior) section of a bivalve specimen showing the flat LV and the downward projecting myophoral plates. C, close-up of B showing the interruption of the (former) inner aragonitic shell layer at the inner slope of the inner shell margin and corrugations (arrow) indicative of a lamellar porous inner structure (due to peeling of the outer shell surface). D, transverse tangential section showing concentric arrangement of the laminations (somewhat obscured by microborings). E, longitudinal section showing the porous lamellar structure (arrow points to the commissure). All from Sopalmo, sample 12077.

gation, might be due to microdissolution, as suggested by Text-figure 14B.

*Distribution of the radial structure in the shell.* The study of the slabs including 14 specimens (Text-fig. 4) shows that the radial pattern is always present on the dorsal side and may invade the anterior and posterior sides whereas the ventral side is usually compact. Only one specimen (i.e. holotype) has an overall radial structure. Image analysis performed on transverse sections ($n = 3$) indicated that the septate structure represents 44–100 per cent of the outer shell surface (see above). The carina found at

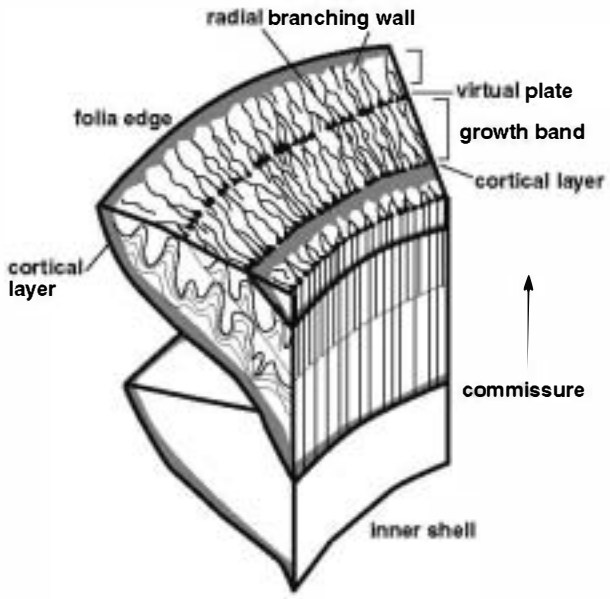



**TEXT-FIG. 10.** *Archaeoradiolites hispanicus*. **A**, transverse section showing the cardinal apparatus; note the lamellar central tooth (RV), the posterior gutter and the anterior tooth in the corresponding socket; Carche, sample 11666. B–C, close-up of the ligament ridge and the adjacent ligament cavity; Sopalmo, sample 12077.




**TEXT-FIG. 11.** *Archaeoradiolites hispanicus*, myophoral apparatus. **A–B**, transverse sections at the same scale showing the bull-horn shape transverse outline of the myophoral plates; Sopalmo, slab 12077. Scale bar represents 0·5 cm.

the junction between the ventral and the anterior shell portions appears to be a critical site for the distribution of the radial structure. Radial walls tend to converge towards the plane of symmetry of the carina, the ventral portion being usually compact or with a limited radially arranged structure, whereas the anterior portion is typic-




**TEXT-FIG. 12.** Three-dimensional sketch of the microstructure of the outer shell layer of *Archaeoradiolites hispanicus* (not to scale).

ally septate (Text-fig. 15). The radial structure characterizes thickened parts of the shell whereas thin parts tend to be compact. This distribution of the radial structure is identical to those of the cellular one in *Eoradiolites*, for instance *E. plicatus* (Conrad) (Douvillé 1913; Chikhi-Aouimeur 1983) (Text-fig. 3B). The relative extent of radial vs. compact structure tends to increase with increasing shell diameter. Some relatively large sections possess a limited septate portion (restricted to the dorsal side) because the section appears to be cut between two consecutive foliae. Because the radial structure is essentially developed within the foliae, the foliated structure is mainly found on the dorsal side, extending to the anterior and posterior sides.

*Ontogenetic development of the radial structure.* The stepwise growth mode of the shell is not only recorded by the tiered fitted funnels but also within the corresponding foliae. Foliae from the initial growth stages show a compact structure (juvenile stage analogous to adult stage of *Archaeoradiolites primitivus*; see Text-fig. 16A), whereas the succeeding ones record an increasing intraskeletal porosity linked to increasing development of the radial walls. Four successive growth stages are illustrated on Text-figure 16C–F, each represented by a close-up of the microstructure showing that the number of radial walls tends to increase as their thickness decreases at each growth step. This trend is documented by a quantitative estimate of the intraskeletal voids measured (using image analysis) for successive foliae and within distinctive parts of each folia. The corresponding curve shows that the onset of each step is marked by a compact structure (i.e. cortical layer) followed by radial walls, but each step records a reduction of the compact structure relative to the radial one, the last having the highest value for intraskeletal voids. The terminal folia marks a size retreat coupled with a relative reduction of the porous structure.

*Archaeoradiolites primitivus* sp. nov.
Text-figures 17–19

1993 *Eoradiolites plicatus* (Conrad); Gallo-Maresca, p. 56, pl. 7, fig. 3.

*Derivation of name.* After the primitive characters of the species.

*Type locality.* Sierra del Carche, south-east of the city of Jumilla, Province of Murcia, south-east Spain (Text-fig. 1B); lat. 38°26′16″N, long. 1°09′58″E.

*Holotype.* Four thin sections and slabs from sample 10769 from Sierra del Carche housed with other materials in the Centre de Sedimentologie-Paléontologie, Université de Provence, Marseille.

*Paratype.* Five thin sections and slabs from sample 15206 from Sierra del Carche (underlying beds to the type level).

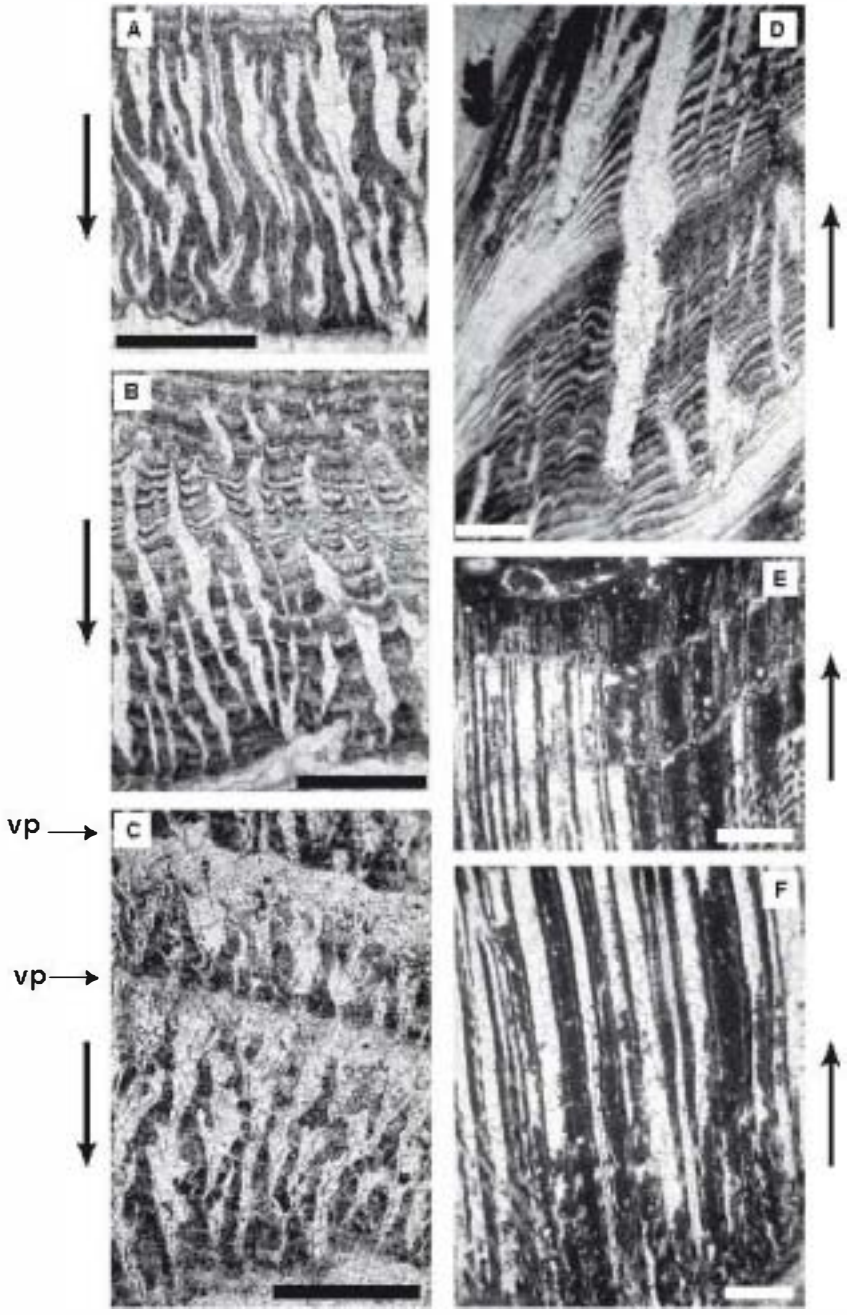
*Additional material.* Five thin sections from sample 5886 from Arudy.

*Specific diagnosis.* Small [max dDV 18 mm, dAP = 18 mm; average diameter (dDV + dAP)/2 = 13 mm], conical, somewhat foliated *Archaeoradiolites*. Radial branching structure restricted to the anterior side, somewhat extending to the dorsal side. Radial bands compact, the anterior wide and flat, fused to the posterior (interband inconspicuous), salient at the posteroventral articulation. Ligament ridge with a low trapezoidal transverse outline, termination concave. LV flat or slightly upward with a porous, laminated structure.

## *Description of material from south-east Spain*

*External characters.* Owing to the absence of isolated specimens the following data derive from the observation of variously orientated sections.

RV conical, from low to high angle, with moderate foliated habit (Text-fig. 18A–B). Transverse outline subrounded at juvenile stage (Text-fig. 17A), elliptical and somewhat lobate dorsally, and anteriorily carinate at adult stage, the carina located at the anteroventral junction (Text-fig. 17B–C). Radial bands with a compact structure, the anterior band flattened and wide, the posterior band salient and corresponding with the posteroventral

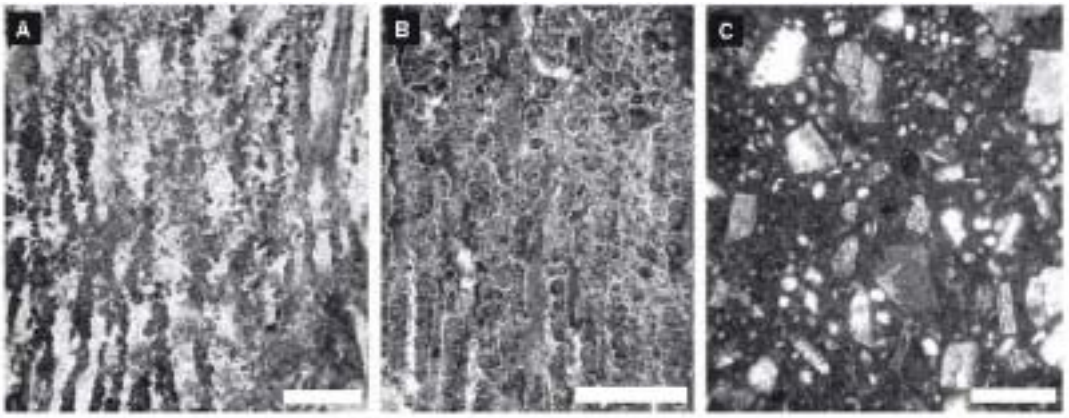



**TEXT-FIG. 13.** *Archaeoradiolites hispanicus*; microstructure of the outer shell layer. A–C, transverse sections showing the radially arranged microbanded branching walls. Note the evolution in B from compact to branching habit and the increase of micritic laminae against (wide) fibrous laminae; vp, virtual plates formed by the distally thickened adjoining radial walls. D, longitudinal radial section showing the discontinuous porous nature of the radial walls. E, tangential folia termination showing the absence of carbonate material covering the radial walls. F, tangential section of the radial walls. Arrows point to growth direction; scale bars represent 0·5 mm.

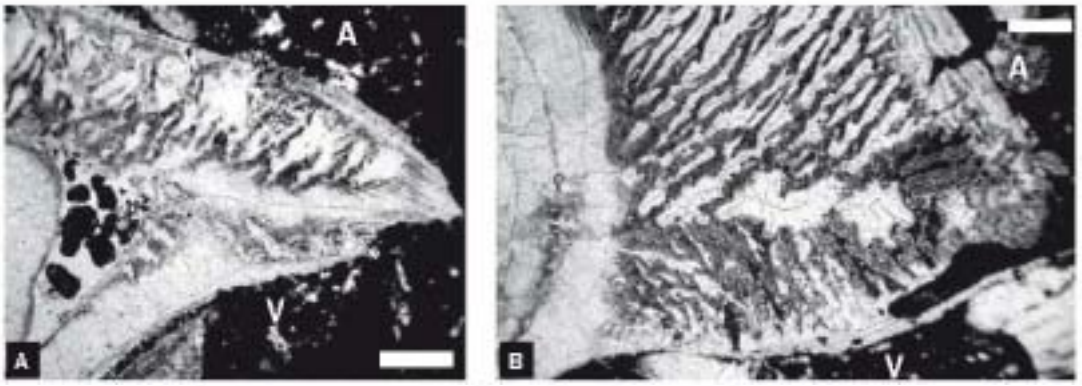
articulation; interband inconspicuous or hardly depressed (Text-fig. 17). Growth surface, extending from the shell edge to the inner margin of the outer shell, slopes inward, so the LV is located in a depression relative to the shell edge. Commissural dimensions fluctuate from 8 to 18 mm (dAP) (average 13 mm) and 9 to 18 mm (dPV) (average 13 mm). LV is flat or slightly concave upward (Text-fig. 18A, C).

*Internal characters.* The cardinal apparatus of the RV includes two sockets changing upward, near the commissure, to gutters and a lamellar central tooth (Text-fig. 17B–C). Myophoral elements of the LV were not observed, except at juvenile stages, showing short asymmetric myophoral plates. Ligament ridge is short, with a trapezoidal to triangular transverse outline.

*Microstructure of the outer shell layer.* Radially orientated branching wall found on the anterior side of the RV tends to bifurcate towards the body cavity (Text-fig. 19A–B). Distal thickening resulting in virtual plates is also observed. Besides the thin elongated and branching walls, short thick and columnar walls are also present, which are interbedded with the compact structure (Text-fig. 19C). Image analysis performed on transverse sections ($n$ = 3) indicates that the septate structure represents 0·42 per




**TEXT-FIG. 14.** *Archaeoradiolites hispanicus*, shell alteration. A, evidence for *in situ* disintegration of radial walls. B, disintegration of radial walls probably due to early dissolution (fitted polygonal elements). C, silt-size elements derived from shell disintegration, within the muddy matrix surrounding a congregation of *Archaeoradiolites hispanicus*. Scale bars represent 0·5 mm.




**TEXT-FIG. 15.** *Archaeoradiolites hispanicus*. A–B, microstructure of the anteroventral carina showing the convergence of radial walls towards the plane of symmetry and the distinctive radial habit of the anterior and ventral side of the carina. A, Carche, sample 11666. B, Sopalmo, sample 12077. Scale bars represent 0·5 mm.

cent of the overall outer shell surface, so significantly less than in *Archaeoradiolites hispanicus*.

Owing to the restriction of the radial walls to the anterior side, dorsoventral longitudinal sections of the RV do not display the septate structure diagnostic of the genus (Text-fig. 17). This is also true for transverse or longitudinal sections of juvenile specimens (Text-fig. 17A). Consequently it is difficult, in some cases, to distinguish *A. primitivus* from *Agriopleura*. The LV shows a porous, laminated structure (Text-fig. 18C).

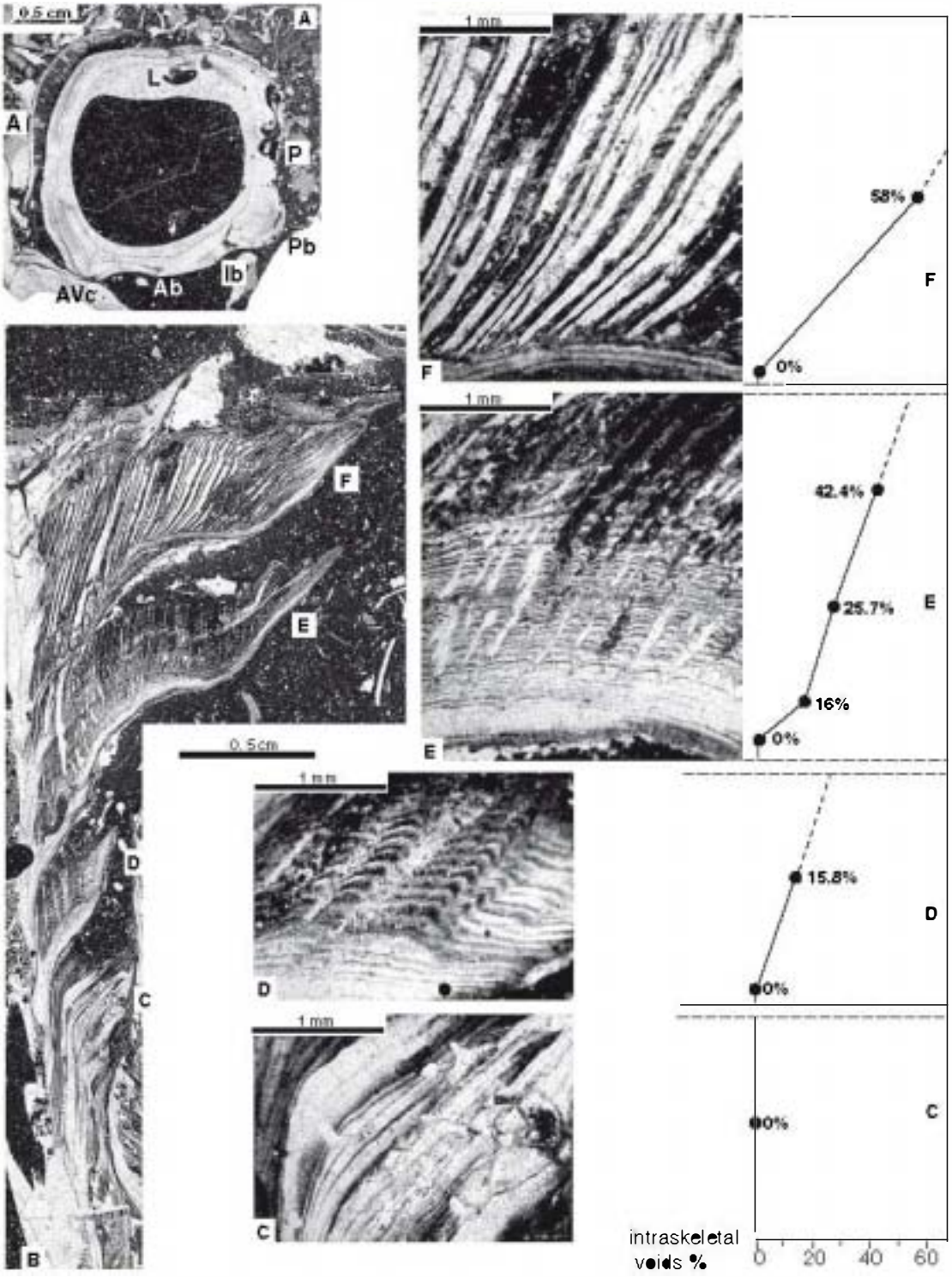
### *Description of the material from south-west France*

Transverse and longitudinal sections cut in samples formerly ascribed to *Eoradiolites* aff. *katzeri* Sliskovic (Masse, 1995) from the Mont-du-Rey Formation in the vicinity of Arudy (Text-fig. 20), attributed to the Gargasian, are assigned here to *Archaeoradiolites primitivus*, based on (1) the overall size and shell habit: conical RV, flat LV; (2) the dominance of compact over septate microstructure of the outer shell layer, the latter being restricted to the anterodorsal side; (3) radial bands poorly defined; (4) RV with moderate foliation.

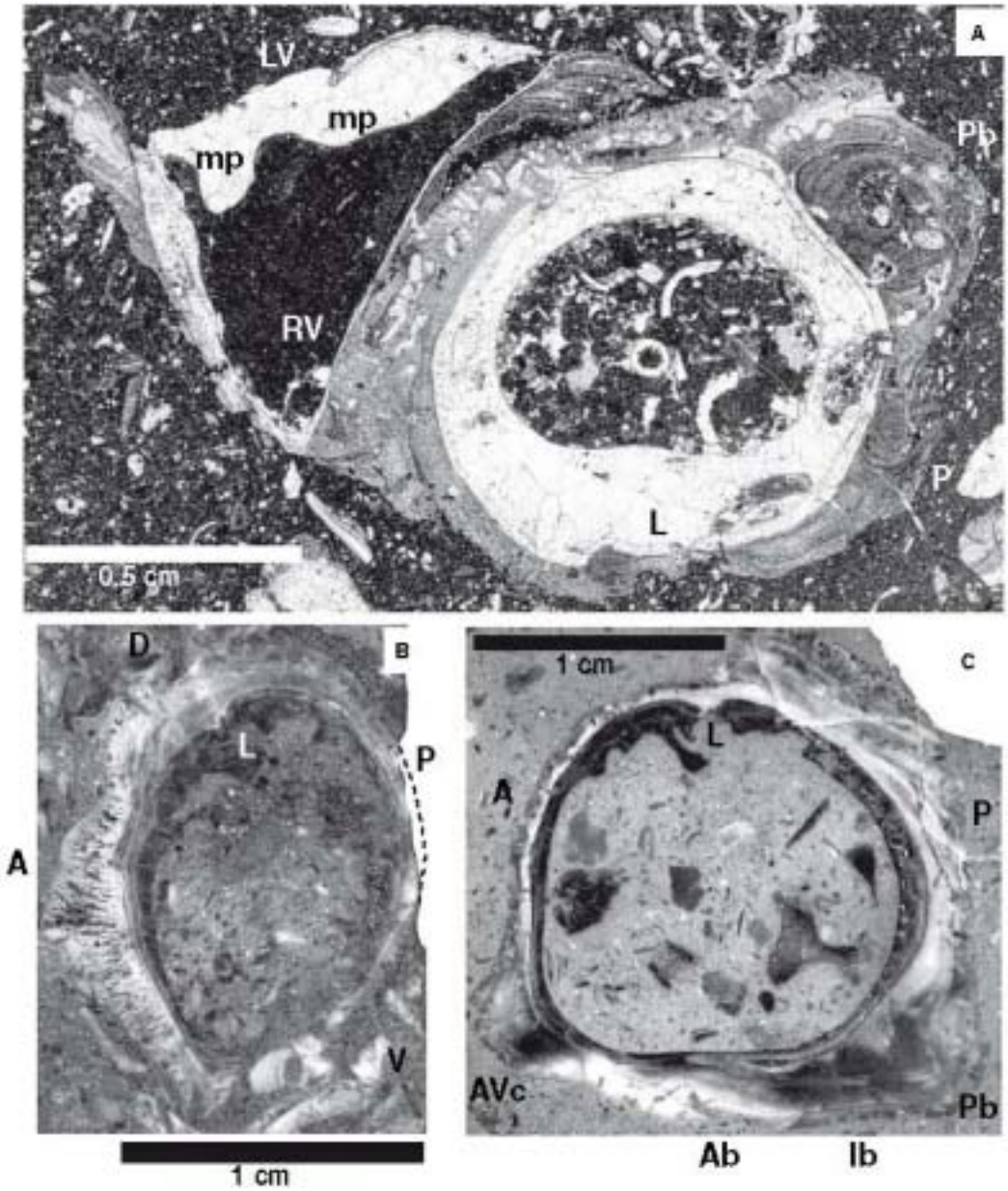
Transverse sections of juvenile specimens and longitudinal sections of adult specimens mainly display a compact outer shell structure. The LV shows corrugations suggesting a septate structure analogous to those of *A. hispanicus*.

*Comparison. Archaeoradiolites primitivus* is similar to *A. hispanicus* but some characters are significantly different: (1) slightly smaller in size, a property that fits with 'Cope's rule' (Cope 1887), predicting that primitive forms are expected to be smaller than their descendants; (2) the foliation of the RV is less pronounced; (3) the radial branching microstructure is restricted to the anterior and the dorsal sides, with the result that the ventral radial bands are always compact; (4) the radial bands tend to be fused, due to the inconspicuous interband; (5) the ligament ridge is smaller.

Owing to the above differences, most of which are related to the more primitive evolutionary state of *A. primitivus* compared with *A. hispanicus*, and their distinctive stratigraphic position (see discussion below),




**TEXT-FIG. 16.** A, *Archaeoradiolites hispanicus* at juvenile stage. B, ontogenetic variation of the radial structure, longitudinal section; Sopalmo, sample 12877. C–F, close-up of B; folise represent successive growth steps with shell structure changing from compact (C), porosity 0 per cent, to highly porous (58 per cent) (F). Each folia records the same trend whereas the porous structure increases with folia size.

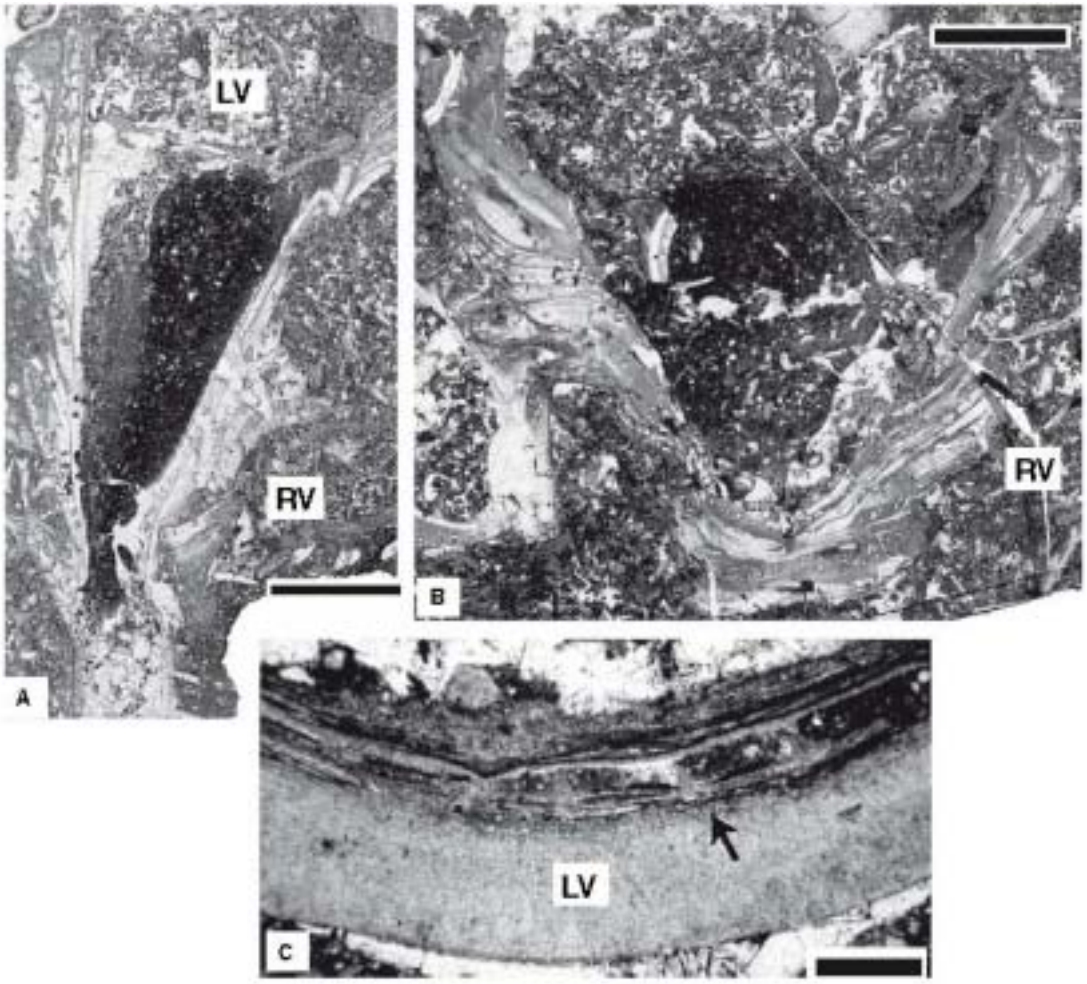



**TEXT-FIG. 17.** *Archaeoradiolites primitivus*. A, two conjoined specimens in transverse (right) and longitudinal oblique (left) section (bivalve); sample 15206. B, transverse section showing the radial structure of the anterior side and the compact structure of the rest of the shell; sample 10769. C, transverse section showing the cardinal feature of the RV and the radial bands; sample 15206. All from Sierra del Carche.

the two species are regarded as phylogenetically related chronospecies.

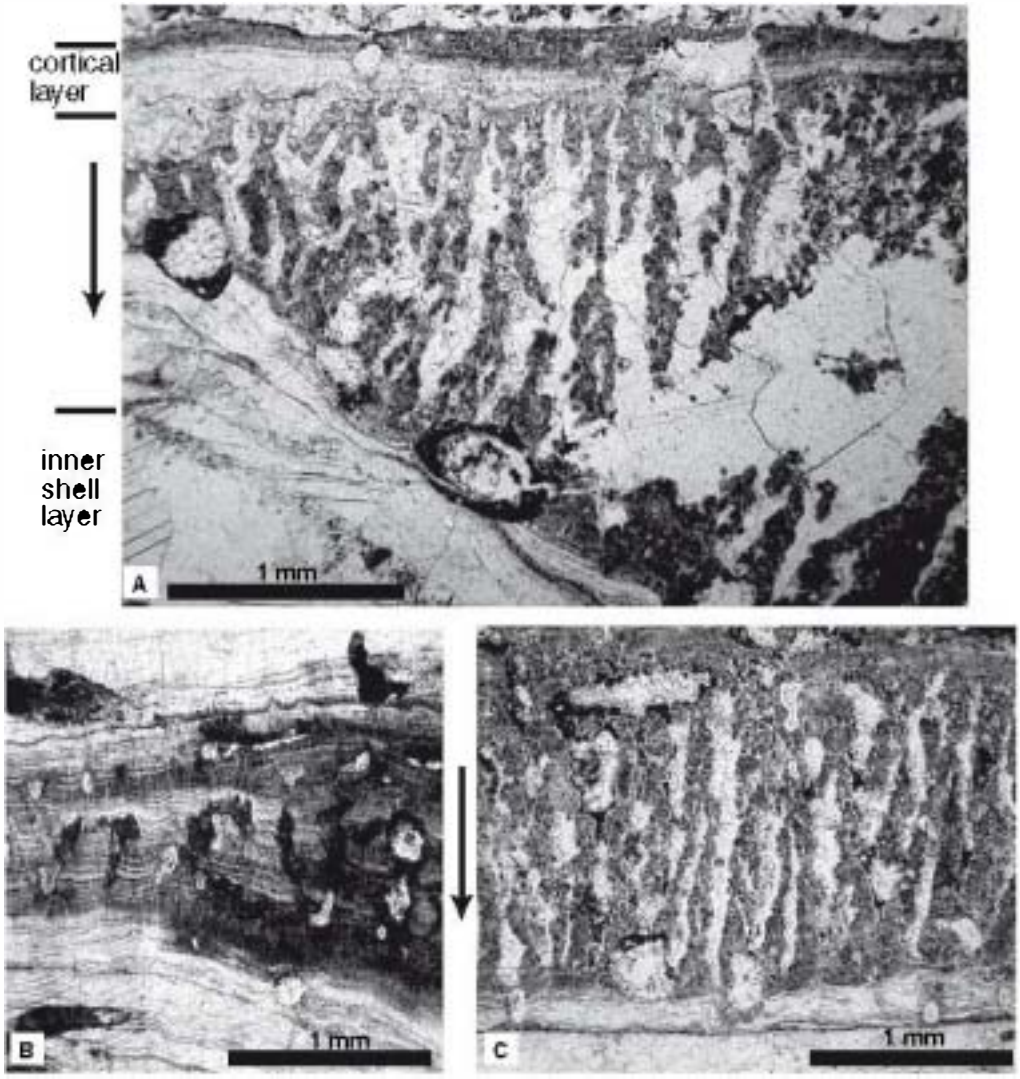
## EVOLUTIONARY ORIGIN OF *ARCHAEORADIOLITES*

*Archaeoradiolites primitivus* is the oldest and most primitive representative of the Radiolitidae yet recognized. Considering *Agriopleura* to be the ancestor (Douvillé 1910; Masse and Philip 1974) or even the origin of Radiolitidae (Paquier 1900; Toucas 1907; Dechaseaux *et al.* 1969) necessitates a discussion of the relationships between *A. primitivus* and the youngest representatives of *Agriopleura*. The attributes of this genus (type species *Agria marticensis* d'Orbigny) include a depressed LV, a compact outer shell layer and the presence on the LV of myophoral bulges (distinct from true plates) flanking elongated




**TEXT-FIG. 18.** *Archaeoradiolites primitivus*. A, longitudinal section showing the conical shell habit of the RV and the flat LV. B, specimen with larger apical angle; note the moderate foliated outer shell surface in both. C, slightly concave LV showing the porous and laminar structure (arrow). All from Sierra del Carche, sample 10769. Scale bars represent 0·5 cm.

teeth. In addition, *Agriopleura* possesses well-defined radial bands and a ligament ridge associated with a ligamental cavity. *Agriopleura* belonging to the *Agriopleura blumenbachi* (Studer) and *Agriopleura marticensis* (d'Orbigny) group are well documented from the Barremian of France and Switzerland (Toucas 1907); they disappeared from the European Tethyan margin in the latest Barremian (Masse 1995). The early Aptian *Agriopleura* species found in Italy (Masse 1992), Lebanon (Douvillé 1913) and the Middle East (Hughes 2003) represent a distinct taxonomic entity (see discussion in Masse 1992). The reference material of *Agriopleura* used for comparison with *Archaeoradiolites* comes from the Shuaiba Formation (Upper Bedoulian) (J.-P Masse, work in progress) of Saudi Arabia and Oman (Skelton and Masse 2000). Two morphotypes are present: conical and cylindro-conical (Hughes 2003), both with a depressed asymmetric LV having grooves running from the commissural margin and converging towards the dorsal side, i.e. to the centre of the valve depression. The ventral bands correspond to a flat, relatively wide anterior band and a salient posterior band forming the posteroventral carina (Text-fig. 21) whereas in the European forms each band possesses a longitudinal depression bound by two fine ridges (Douvillé 1910, 1918). The organization of the radial bands of *Archaeoradiolites hispanicus* is nearly identical to the late Bedoulian representatives of *Agriopleura* from the Middle East. Differences between the latter and *Archaeoradiolites* include the following: (1) in *Agriopleura* the edges of the RV and LV are conjoined (Text-fig. 21), whereas the LV of *Archaeoradiolites* is located within the depression formed by the sloping inward outer shell margin (Text-fig. 9); (2) whereas the size of Arabian forms of *Agriopleura* depends on the morphotypes (the conical ones tend to be smaller than the cylindro-conical ones) the average size is greater than that of *Archaeoradiolites* species; (3) myophoral plates are present in Arabian forms of *Agriopleura* (Text-fig. 21), a character by which




**TEXT-FIG. 19.** *Archaeoradiolites primitivus*, structure of the outer shell layer, Sierra del Carche, sample 10769. Transverse section cut into a specimen to show various structural habits. A, radial branching walls (anterior side). B, short and thick banded radial walls associated with a compact structure. C, radial branching walls showing some trends towards disintegration. Arrows indicate the direction of growth.

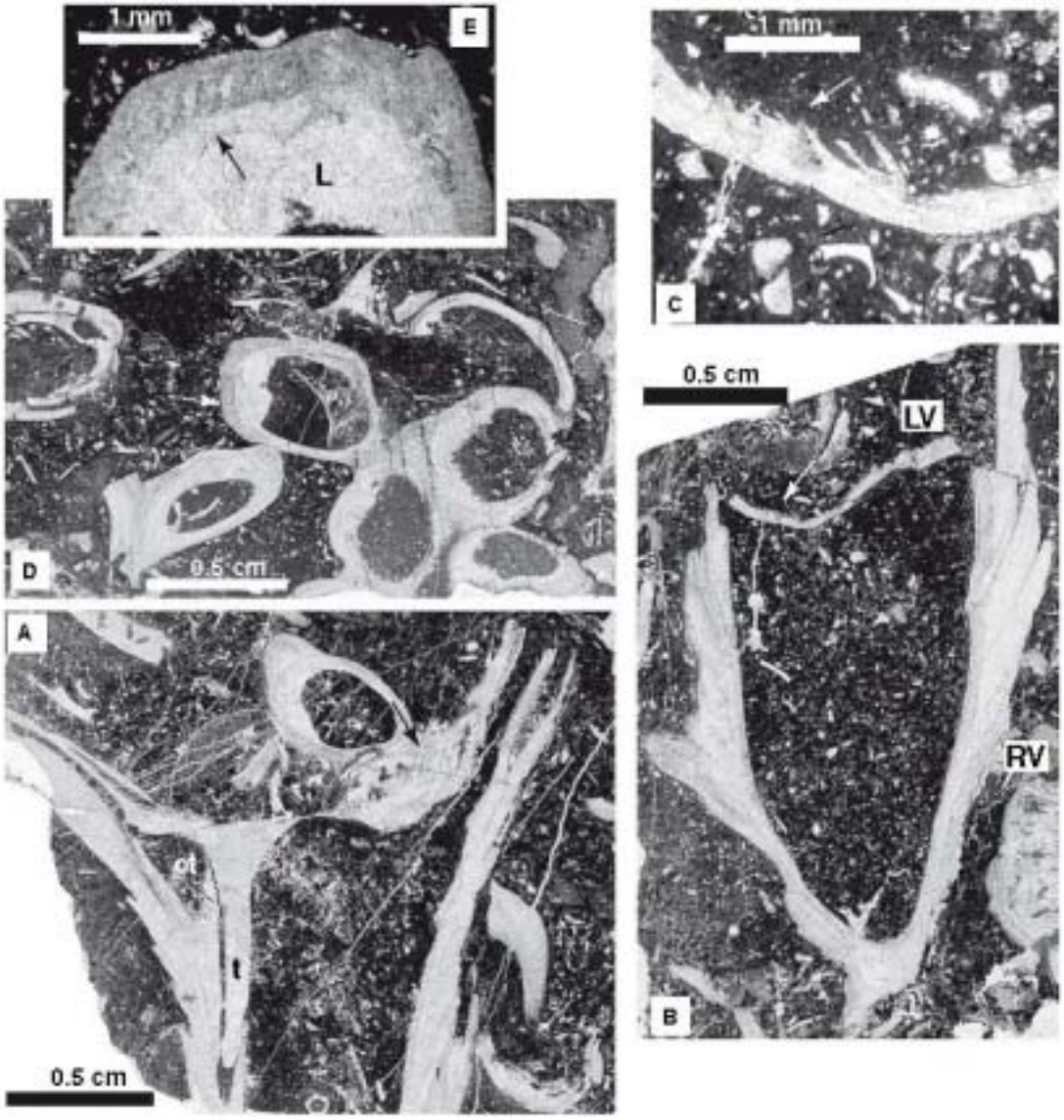
they differ from their European homologues, whereas their dorsoventral extent is more limited than those of *Archaeoradiolites* (i.e. *A. hispanicus*); and (4) the outer shell structure of *Agriopleura* is compact throughout its development.

Comparison between *Archaeoradiolites* and the late Bedoulian representatives of *Agriopleura* (instead of those of Barremian age) provides additional evidence for the close similarity of the latter genus with primitive Radiolitidae, noted mainly as *Eoradiolites* by many authors (Toucas 1907; Dechaseaux *et al.* 1969 among others).

To conclude, notwithstanding generic-level differences between Arabian forms of *Agriopleura* and *Archaeoradiolites*, similarities between the two genera suggest derivation of the latter from the former in accordance with earlier hypotheses regarding *Agriopleura* as the root for Radiolitidae. Size reduction associated with the onset of *Archaeoradiolites* and the absence of septate microstructures in the juveniles of *A. primitivus* suggest derivation from *Agriopleura* through paedomorphosis, a process documented in some rudist lineages (Gourrat *et al.* 2003).

## EVOLUTIONARY RELATIONSHIPS WITH *EORADIOLITES*

The erection of *Archaeoradiolites* necessitates a discussion of the relationships between this genus and *Eoradiolites*, which up to now was considered the progenitor of the

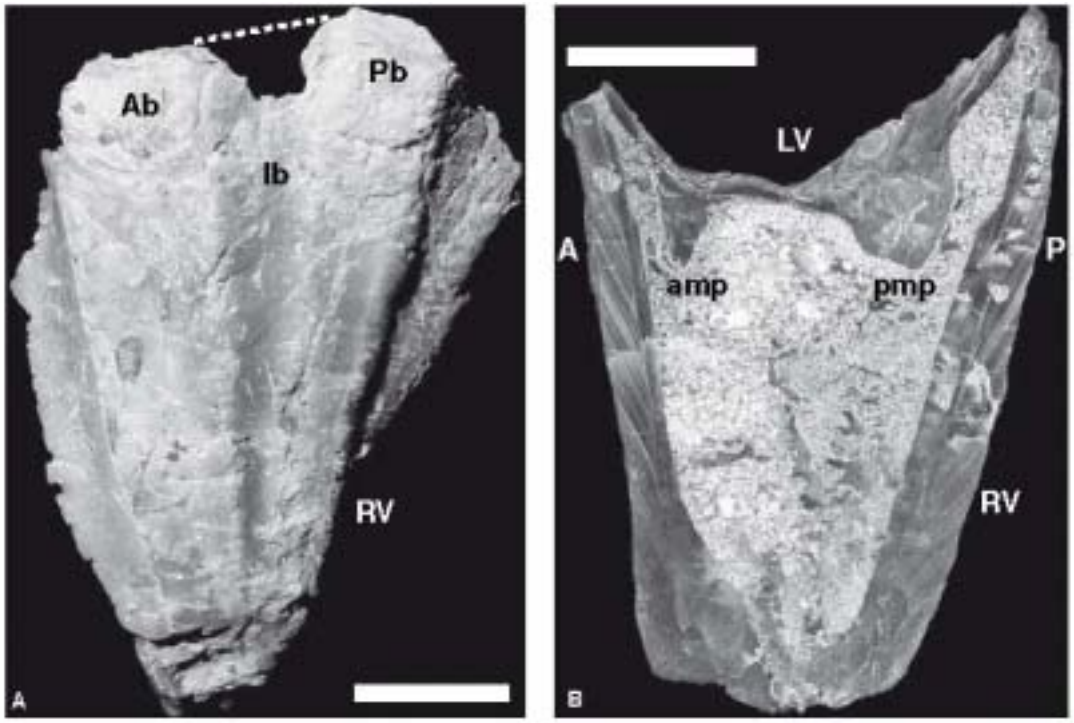



**TEXT-FIG. 20.** *Archaeoradiolites primitivus*, Arudy, sample 5886. A, longitudinal dorsoventral section of a hivalve specimen showing two teeth and the deprassed LV. B, as for A, anteroposterior ventral section; arrow points to corrugations and the relicts of the laminated microstructure of the LV. C, close-up of the corrugations in B. D, transverse section of a congregation. E, close-up of the dorsal side showing the radial walls (arrow).

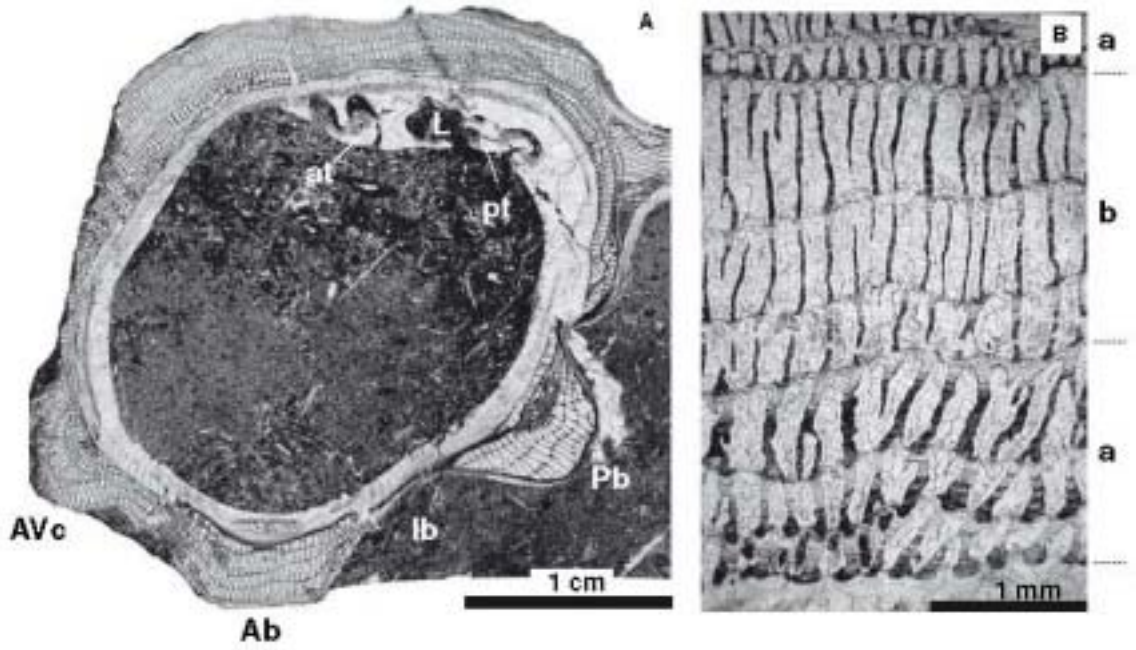
Radiolitidae (see discussion above). Stratigraphic evidence documents the coexistence of *Archaeoradiolites* and the first representatives of *Eoradiolites* in the Upper Gargasian of Sierra del Carche (Text-fig. 2); the two genera are still coeval in the Clansayesian from south-east Spain and southern France. The definition of *Eoradiolites* must combine the organization of the radial bands (to follow Douvillé's view) and the presence of the quadrangular cellular habit of the outer shell layer, built of walls and plates *s.s.* (instead of virtual plates).

We have identified specimens found in the uppermost Gargasian of the Sierra del Carche, with a cellular organization as *Eoradiolites* sp. (Text-fig. 22). The cellular fabric consists of: (1) radially branching walls with a distal inflation and a pronounced microbanding, associated with micritic or relatively thick banded plates; (2) thin, elongated, usually unbranching walls interrupted by micritic plates. The radial branching habit closely resembles that of *Archaeoradiolites*, whereas virtual plates are replaced by plates *s.s.* This type of microstructure is found, for instance, on the dorsal side of *Eoradiolites plicatus* (Text-fig. 3B).

Likewise we assign to *Eoradiolites* sp. a form formerly placed in *Eoradiolites plicatus* by Masse *et al.* (2002) (see

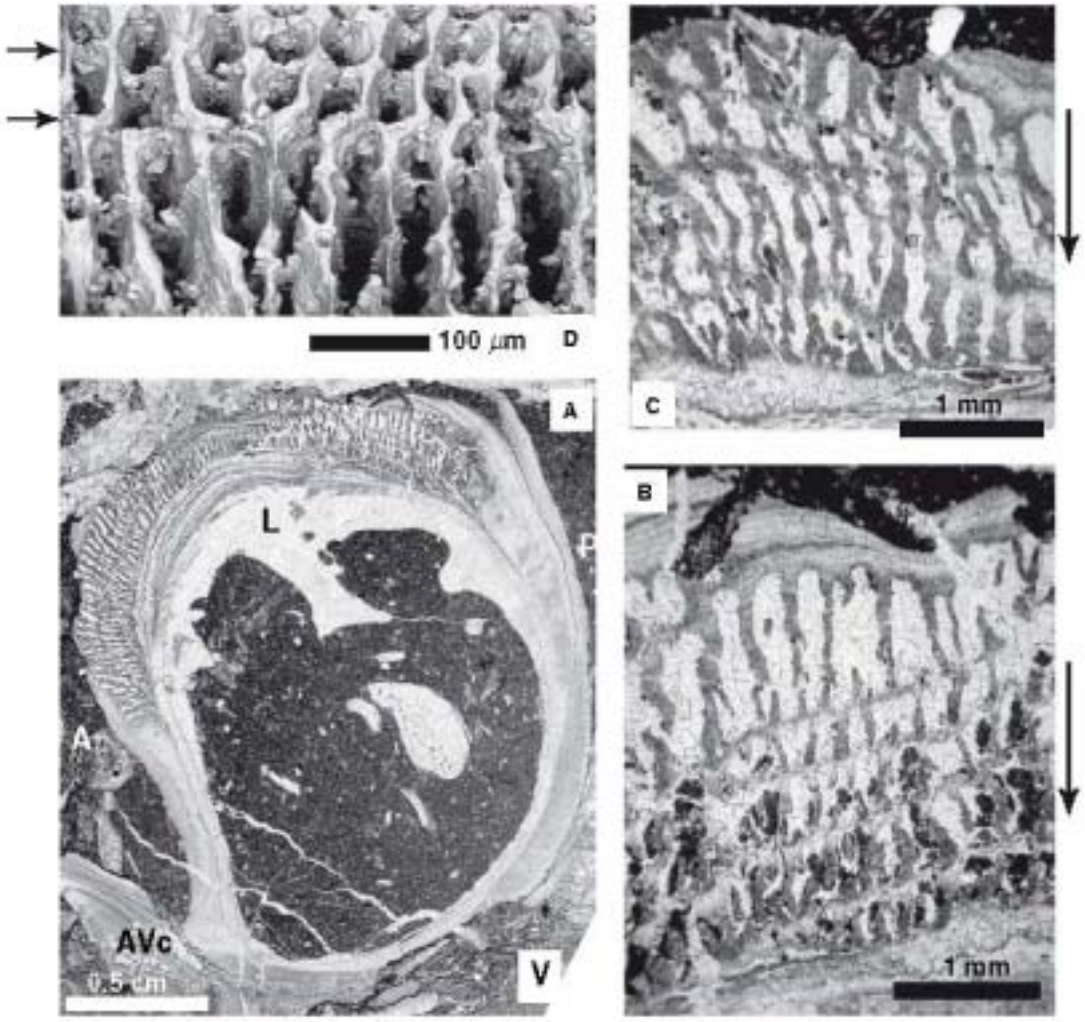



**TEXT-FIG. 21.** *Agriopleura* sp., Upper Bedoulian Shuaiba Formation, Shayba field, Saudi Arabia. A, ventral view showing the configuration of the radial bands. B, longitudinal section of the same specimen showing the myophoral plates. Scale bars represent 1 cm.




**TEXT-FIG. 22.** *Eoradiolites* sp., Upper Gargasian, Sierra del Carche, sample 11672. A, transverse section showing the overall organization. B, close-up of the anterodorsal area showing radial branching structures (a) and quadrangular cells (b), both with plates.

fig. 8, p. 531) (Text-fig. 23) found in the Upper Aptian of the Zonguldak region (western Black Sea, Turkey). In this form the cellular structure is limited to the dorsal side and consists of radial branching walls with an inward distal thickening plus micritic walls, locally somewhat incomplete. Although this form appears to be identical to




**TEXT-FIG. 23.** *Eoradiolites* sp., Upper Aptian, Cengellidere Formation, Zonguldak region, Turkey, sample 14146. A, transverse section showing the restriction of the cellular structure on the dorsal side. B–C, close-up of the same specimen showing cellular structure (B) and incomplete cellular structure with radial branching walls closely resembling those of *Archaeoradiolites* gen. nov.; arrows indicate the direction of growth. D, SEM [image back scattering electrons (BSE) 0·5 tor/chamber] view of a silicified specimen (carbonate has been removed) showing septate elements (walls) and incipient plates (arrows), sample 14148.

*Archaeoradiolites*, the presence of plates warrants its placement in *Eoradiolites*.

## ONSET OF THE RADIOLITIDAE IN THE EARLY GARGASIAN: BIOLOGICAL AND PALAEOENVIRONMENTAL SIGNIFICANCE

The onset of the Radiolitidae is associated with major global changes responsible for the mid-Aptian biological crisis (Masse and Philip 1986; Masse 1989; Skelton 2003) marked by the extinction of 42 per cent of the generic biodiversity and 57 per cent of the specific diversity of the cardinal benthic forms (foraminifera, dasycladalean algae and rudists) thriving on shallow carbonate platforms. Aside from the reduction in the spatial distribution of carbonate platforms, changes in chemical properties of the ocean (Masse 1989) coupled with a rise in $CO_2$, an increase in productivity and changes in seawater saturation with respect to aragonite (Bergen 1998; Weissert *et al.* 1998) have been suggested. The drop in biodiversity started in mid Bedoulian times and continued across the Bedoulian/Gargasian boundary (Masse 2003). The anoxic event OAE 1a (Arthur *et al.* 1990), which occurred in the Hambrovi Subzone of the Deshayesi Zone (Upper Bedoulian) and pre-dates the extinction peak (the Furcata/Tobleri boundary event), was not

responsible for the biological crisis for that reason, but was involved in the biodiversity decline preceding the extinction peak.

Lowering of the Mg/Ca ratio is a good candidate to account for a change from an 'aragonite regime' to a 'calcite regime' (Sandberg 1983; Stanley and Hardie 1998), expressed by dasycladalean algae, aragonitic foraminifera and caprinid rudists. Linking the evolution of bivalves and the modification of seawater chemistry has been documented by Harper *et al.* (1997), who stressed the difficulty of maintaining aragonite shells in 'highly corrosive' calcite seas. By contrast with the 'Hardie model' (Hardie 1996; Steuber 2002), which predicts that a modification from an aragonite to a calcite regime occurs over time periods of the order of 10 myr, data from the mid-Aptian suggest a rapid change (< 0·5 myr). Similar short-term changes were also proposed by Pomar *et al.* (2004) for the Miocene. For Stanley and Hardie (1998) the development of the Radiolitidae was not a direct consequence of the mid-Cretaceous shift from aragonite to calcite seas. They suggested that the decline of the aragonitic corals, resulting from a decrease in the Mg/Ca ratio of seawater, opened the way for rudists in the highly competitive reef environments. However, as shown earlier (Scott *et al.* 1990; Gili *et al.* 1995), rudists and corals were thriving in distinctive environments so that competition between the two groups must be ruled out. Therefore, the development of the Radiolitidae in the Late Aptian appears to have been independent of the evolution of scleractinian corals, but has much to do with: (1) the vacant space left by the extinct Early Aptian Caprinidae; and (2) the onset of a calcite regime, which was also advantageous for other coeval rudists: Polyconitidae (*Polyconites*, *Horiopleura*), Caprotinidae (*Caprotina*) and Monopleuridae ('*Agriopleura darderi*', '*Petalodontia*'), all with a thick outer calcitic shell layer by comparison with the inner aragonitic shell layer (Masse *et al.* 1998).

The development of a porous, septate, structure in the calcitic outer shell layer of the Radiolitidae might be compared with the development of the canaliculate structure observed in the originally aragonitic, inner shell layer of the Caprinidae. In both groups the strategy appears likely to have minimized the cost of metabolic energy used for shell production (Douvillé 1904; Palmer 1983) and may have facilitated quick growth. As shown in modern ostreids (Chinzei 1995) vesicular shells allow soft-bottom bivalves to float on muddy bottoms, an advantage for solitary individuals. This hypothesis looks likely for Late Aptian Radiolitidae, which are essentially associated with wackstones (or very fine packstones). Another advantage of septate structures is the potential to resist shell breakage (Skelton 1976). A striking feature of *Archaeoradiolites* species is the high density of sponge (*Cliona* type) borings, which are restricted to shell portions with a compact microstructure, i.e. portions with radially arranged walls are free of borings (Text-fig. 7). Data from the Recent show that clionid sponges tend to infest various living or dead carbonate substrates, either compact or porous, but avoid parts with a large pore size (Schönberg 2002). The distribution of clionid borings in *Archaeoradiolites* may only reflect this biological need; nevertheless, it is necessary to be aware of the global context of the coeval high seawater productivity (see above). High productivity is known to promote an increase in sponge biomass and therefore an increase in infestation of carbonate substrates (Rose and Risk 1985). From the foregoing it is suggested that the acquisition of a septate structure by *Archaeoradiolites* might have been advantageous for avoiding detrimental strong infestations by clionid sponges. This strategy has already been discussed by Skelton (1976) for caprinid rudists. An alternative strategy, used by accompanying rudists, appears to have been an increase in shell thickness (e.g. *Pseudotoucasia*, *Horiopleura*) or the development of tubular structures at the interface between the outer and inner shell layer as, for instance, in '*Agriopleura*' *darderi* (Masse and Philip 1974).

The development of *Archaeoradiolites* communities, which started with *Archaeoradiolites primitivus* in the Lower Gargasian, was studied at the Sierra del Carche. This study was based on quantitative estimates of the following ecological attributes (Fenerci-Masse *et al.* 2004): packing density (number of individuals in a 100-$cm^2$ vertical surface); packing-index (number of individuals in lateral contiguity, expressed in per cent); coverage (per cent of cumulative surface covered by individuals on a given bedding plane); and skeletal contribution (ratio of shell material vs. sediment in per cent).

Three steps were recognized in the evolution of radiolitid assemblages of *Archaeoradiolites primitivus*: (1) isolated specimens found with a requieniid-dominated community (*Pseudotoucasia*) in the lowermost Gargasian (the paucity of individuals did not permit quantitative estimates); (2) low-density assemblages, the quantitative attributes of which (including packing-index, packing density and coverage) fluctuate between 0 and 0·3, associated with Requieniidae, in the upper part of the Lower Gargasian; (3) a radiolitid community with a relatively high packing-index and packing density (18.5% and 16 individuals, respectively), moderate coverage (35%) and macroskeletal contribution (16%), *Archaeoradiolites primitivus* being the only member of this community (Bed 10769).

In assemblages of *Archaeoradiolites hispanicus* from the uppermost Lower Gargasian of Sopalmo (type level) (see slab 12077) and Almansa (bed 10920), packing density ranges from 10 to 40, packing-index from 26 to 46 per cent, and coverage between 55 and 70 per cent, the skeletal

contribution being about 50 per cent. These high values indicate that this species played a significant role in carbonate production and possessed a constructional potential somewhat higher than that of hippuritid-dominated lithosomes of the Late Cretaceous, which have lower packing density and coverage (Vilardell and Gili 2003). As for the hippuritid lithosomes, Gargasian radiolitid-dominated beds lack relief, and their average bed thickness is reduced (less than 1 m), but they may, at least locally, build rigid frameworks.

## STRATIGRAPHIC AND GEOGRAPHICAL DISTRIBUTION OF *ARCHAEORADIOLITES*

*Archaeoradiolites primitivus* has been recorded from the upper part of the *Dictyoconus pachymarginalis* interval (Lower Gargasian) below the Montemayor Sands at Sopalmo, whereas it is present in beds overlying these sands in the *Orbitolinopsis reticulata/O.? aquitanica* interval (Upper Gargasian) from the same locality and surrounding sites of the Jumilla area. One small specimen comes from the lower part of the Gargasian beds of Sierra del Carche. This species was also found in the Caroch area and at Almansa in Upper Gargasian beds. In south-west France *Archaeoradiolites primitivus* was found in the Gargasian, probably the lower part, of the Arudy area, near Pau.

*Archaeoradiolites hispanicus* has been recorded in Upper Gargasian beds from south-east Spain: Sierra del Carche, Sopalmo, Almansa and Caroch. In the Sierra del Carche this species is still present in the Clansayesian *Pseudochoffatella cuvillieri*-bearing beds.

To conclude, the stratigraphic distribution of the two species of *Archaeoradiolites* may be summarized as follows: (1) *Archaeoradiolites primitivus* is found alone in the Lower Gargasian and together with *Archaeoradiolites hispanicus* in the uppermost Lower Gargasian and the lowermost Upper Gargasian; (2) *Archaeoradiolites hispanicus* is found with primitive representatives of *Eoradiolites* in the Upper Gargasian, then co-occurs with advanced *Eoradiolites* [the so-called *Eoradiolites cantabricus* (Douvillé)] group in the Clansayesian (Masse *et al.* in press).

Our data indicate that *Archaeoradiolites* appears to be restricted to south-west France and south-east Spain, i.e. the western part of the European Tethyan margin. Nevertheless, primitive *Eoradiolites* from the western Black Sea coast of Turkey, close to *Archaeoradiolites*, suggests a direct derivation of the former from the latter and therefore possibly the existence of *Archaeoradiolites* in the East European Tethyan margin, known to possess strong palaeobiogeographical affinities with the West European domain during the Barremian–Aptian (Masse *et al.* 2002).

## CONCLUSIONS

A new genus, *Archaeoradiolites*, is described from the Upper Aptian of south-east Spain and south-west France, characterized by the microstructure of the outer shell layer of the RV, which consists of radial branching walls and virtual plates formed by adjoined, inflated terminations of the radial walls. The LV is flat and possesses a laminated concentric microstructure. The other organizational attributes, myophoral organs, radial bands and ligament ridge, are identical to those of *Eoradiolites*.

*Archaeoradiolites* includes two species, *A. hispanicus* (type species) and *A. primitivus*, distinguished by the relative development of the radial branching walls in the outer shell layer microstructure, mainly restricted to the anterior side in *A. primitivus* and extending to the anterior, dorsal and posterior sides in *A. hispanicus*. In *A. hispanicus* the RV is strongly foliated, owing to the tiering of fitted funnels, and shows pronounced ontogenetic variations regarding the microstructure of the outer shell layer. In *A. primitivus* the foliation of the RV is less pronounced and there are also ontogenetic variations: the juveniles are essentially compact.

*A. primitivus* is found in the Lower Gargasian and the lowermost Upper Gargasian; *A. hispanicus* is present in the uppermost Lower Gargasian and extends to the Clansayesian. This distribution gives to the two species of *Archaeoradiolites* potential for characterizing and subdividing the Upper Aptian.

*Archaeoradiolites* appears to be the direct descendant of *Agriopleura*, probably through paedomorphosis. It was the progenitor of *Eoradiolites*, the cellular, quadrangular microstructure of which departs from that of *Archaeoradiolites*.

The onset of the Radiolitidae is associated with major global changes and a strong biological crisis in mid-Aptian times. The acquisition of an outer shell layer of porous, septate microstructure may relate to strategies combining the minimizing of metabolic energy for shell production, the provision of some ability to float on muddy bottoms, and an increase in resistance to shell breakage and in ensuring protection against sponge boring. This may account for the ability of *Archaeoradiolites* to form densely packed communities with a significant bioconstructional character, acquired during the earlier phase of the radiation of the family Radiolitidae in less than 1 myr after the mid-Aptian extinction event.

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